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THE

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# 1.—The Environment of the Quokka *(Setonix brachyurus)* in the Darling Range, Western Australia

by G. M. Storr*

*Manuscript received—21st May, 1963*

The more constant environment of the mainland quokkas and their maintenance of good condition through the summer are contrasted with the seasonal extremes and loss of condition on Rottnest.

## Introduction

Owing to summer drought and the low capacity of the sandy soil for retaining water, most Rottnest plants grow only in winter and spring. They consequently contain much less water and protein in March and April than in August and September (Storr 1961). As their food deteriorates, so the quokkas rapidly lose weight, and their fur becomes increasingly frowsy and verminous. In contrast, a small series of quokkas from the Darling Range north of Jarrahdale showed no significant seasonal variation in condition (Sadleir 1959). It therefore became important to study the environment of these quokkas, if only for a better understanding of the defects of Rottnest.

## Habitat

At Jarrahdale (and apparently everywhere on the mainland) quokkas live in densely vegetated swamps. Some water is always present, whereas on Rottnest it is restricted in summer to a few small seepages round the salt lakes and the coast. Aggravating the prevailing absence of fresh water on Rottnest is the scarcity of good shade. On hot days the temperature in a typical quokka shelter on Rottnest exceeded official shade temperatures by 9-22°F, whereas at Jarrahdale it was 5-12° lower than official readings (Sadleir 1959).

The lower than shade temperature at ground level in Jarrahdale swamps is due to the great depth and stratification of the plant cover. The lowest story consists of tall sedges, *Cladium preissii* and *Lepidosperma tetraquetrum*, interspersed with shrubs of *Acacia divergens*, *A. alata*, *Oxylobium lineariifolium*, *Mirbelia dilatata*, *Bossiaea biloba*, *Aotus cordifolia*, and *Boronia elatior*. Next is a layer of tall shrubs, mostly *Agonis linearifolia*, whose canopy is usually closed, and through which emerge scattered small trees; *Melaleuca parviflora*, *Banksia littoralis*, and *Albizzia distachya*. Above all these are the tall eucalypts, *E. patens* and *E. calophylla*.

Quokka runways (more appropriately, tunnels) intersect the sedge zone, and it is here that the animals hide up during the day. At night they come out to feed not only in the swamp itself but also along its edges, where the ground cover is much lower and more open. The vegetation of these marginal flats consists principally of small sedges, *Cladium laxum*, *Tetrariopsis octandra*, *Cyathochaete avenacea*, and *Lomandra endlicheri;* perennial herbs, *Thomasia foliosa*, *T. pauciflora*, and *Trachymene compressa*; and the fern *Pteridium aquilinum*. As the land rises the ground cover quickly merges with the highly sclerophyllous undershrubbery of the jarrah forest.

The vegetation of the swamps and their margins is thus dominated by sedges, perennial herbs, and leguminous and myrtaceous shrubs. In contrast to Rottnest, succulents, i.e. Chenopodiaceae, Aizoaceae etc., are completely absent. Grass is rare and represented by a single species (*Tetrarrhena laevis*). Indigenous annual herbs are an insignificant element in the flora, and no alien species have become established where the vegetation remains undisturbed.

## Seasonal variation in nutrients

The terminal foliage of plants growing in and beside a quokka swamp near the source of Manjedal Brook (3 miles north of Jarrahdale) were analysed for water and protein on various occasions in 1958-9. The results are set out in Table 1, an asterisk prefixing species known to be eaten by quokkas (these were found by searching the vegetation along runways for evidence of browsing).

Almost all the shrubs and herbs growing on the dry lateritic soil above the swamp have a winter growth regime. Fragmentary data (not tabulated) indicate that water and protein levels, as on Rottnest, are considerably higher in spring than autumn.

Plants growing on the clayey soil of the marginal flat have generally a similar regime; though there is no great contrast between spring and autumn values of water and protein. *Pteridium* alone of the seven species has summer rather than winter growth, without, however, marked seasonal variation in nutrients.

Of the eleven species growing in water or permanently damp soil, only two, *Aotus* and *Oxylobium*, have a winter growth regime; but again seasonal fluctuation in nutrients is quite small. Four species, *Acacia alata*, *Albizzia*, *Eucalyptus patens*, and *Mirbelia*, have a summer growing season; while the remainder, including the two sedges, scarcely change in protein and water content.

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## TABLE 1

*Crude protein content (% dry weight), with water content (% wet weight) in brackets, of terminal foliage of common plants at Manjedal Brook. Known food plants are asterisked.*

| | June and July | October | January | March |
|---|---|---|---|---|
| Swamp Species | | | | |
| *Acacia alata* | 10·6 (54) | | 11·8 (61) | 13·7 (58) |
| **Agonis linearifolia* | 6·9 (58) | 8·1 (58) | 6·4 (58) | 8·4 (59) |
| *Albizzia distachya* | 15·3 (62) | | 16·0 (61) | 20·4 (65) |
| **Aotus cordifolia* | 9·5 (72) | | | 7·3 (59) |
| *Astartea fascicularis* | 5·4 (53) | 7·0 (56) | 4·6 (50) | 4·8 (52) |
| *Banksia littoralis* | 5·7 (53) | | 5·7 (54) | 6·0 (56) |
| *Cladium preissii* | 4·5 (40) | 4·2 (40) | 4·0 (43) | 4·3 (44) |
| *Eucalyptus patens* | | 6·3 (54) | 8·3 (66) | 7·8 (65) |
| **Lepidosperma tetraquetrum* | 4·8 (64) | 4·7 (61) | 5·0 (63) | 4·4 (63) |
| *Mirbelia dilatata* | 8·7 (68) | | 9·7 (66) | 12·2 (73) |
| **Oxylobium linearifolium* | 12·9 (64) | | 11·6 (59) | 12·2 (63) |
| Marginal Flat Species | | | | |
| *Bossiaea biloba* | | 8·3 (58) | 7·7 (45) | 6·8 (38) |
| **Cladium laxum* | 4·8 (60) | | 4·8 (64) | 3·9 (56) |
| *Pteridium aquilinum* | 6·3 (52) | | 6·6 (55) | 7·0 (52) |
| *Tetrariopsis octandra* | | 4·7 (44) | | 3·3 (41) |
| **Tetrarrhena laevis* | 9·8 (61) | 7·2 (62) | 6·7 (53) | 6·1 (53) |
| *Thomasia foliosa* | 6·7 (49) | 8·6 (57) | 7·6 (59) | 4·3 (50) |
| *Thomasia pauciflora* | 5·9 (49) | 8·6 (53) | 6·2 (56) | 7·2 (54) |

At all seasons there are some plants in or beside the swamp putting on fresh growth. Because of this and the small intra-specific fluctuation in nutrients, there will likewise be little seasonal variation in the quokkas' intake of water and protein. To illustrate this constancy the data in Table 1 have been averaged and graphed (Fig. 1). Although these averages are not necessarily the same as those of their actual food, the latter must vary in the same way and indeed cannot be greatly different. For comparison, mean water and protein content of the food of Rottnest quokkas are also graphed (data from Storr 1961).

### Discussion

The absence of marked seasonal fluctuation in the condition of Jarrahdale quokkas is undoubtedly due to their relatively stable plane of nutrition. What is not so easily explained is how they maintain good condition on a diet that can be little richer in protein than that of Rottnest quokkas at its worst. Perhaps their DMI (daily intake of dry matter) is considerably higher than on Rottnest, where it averages 45 g in adult males (Storr 1963), a much lower rate than in captive quokkas eating dry food but supplied with unlimited water (*cf.* Calaby 1958, and Bentley 1960). Since DMI in ruminants falls as the water content of their food exceeds 80% (Dodsworth and Campbell 1952), the intake of Rottnest quokkas could well be depressed by the succulence of their food (75-85% water).

A perusal of the data in Table 1 shows that the mean water content of the food at Jarrahdale cannot be much greater than 60% throughout the year. It is thus possible that a higher DMI more than compensates for the relatively low protein content of the food of Jarrahdale quokkas.

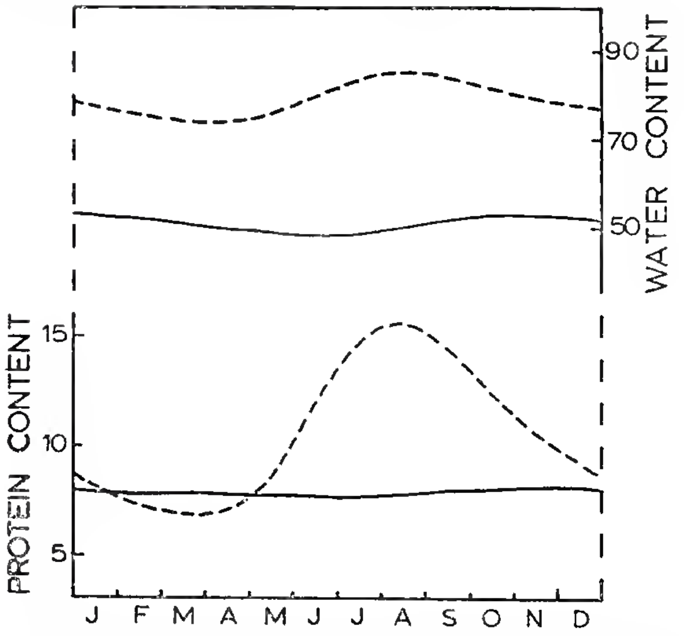

Fig. 1.—Seasonal changes in protein and water content of vegetation. Full lines, plants at Manjedal Swamp; broken lines, food plants of Rottnest quokkas.

### Acknowledgments

The work was financed by research grants from the CSIRO and University of Western Australia. The writer is grateful to Mr. R. D. Royce (Government Botanist) for the identification of plants; to Mr. S. Gorman (Government Chemist) for protein determinations; to his colleagues, Drs A. R. Main and R. M. Sadleir, for advice and assistance in the field; to Prof. H. Waring for criticism of the manuscript; and to Dr Main for supervising the work.

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# 2.—An Ordovician Cystoid (Pelmatozoa, Echinodermata) from Western Australia

By Ida A. Brown*

*Manuscript received.—18th June, 1963*

The paper describes a new species of *Cheirocrinus* Eichwald from the Ordovician of the Kimberley Division, Western Australia. This is the first cystoid (Pelmatozoa, Echinodermata) to be described from Australia, and the first record of this genus from the Southern Hemisphere.

## Introduction

There are comparatively few records of recognizable fossil Pelmatozoa (Echinodermata) in Australia, although "crinoidal" limestones are relatively common within the Palaeozoic sequence. This is the first description of a cystoid; a few blastoids have been described from the Upper Palaeozoic or eastern Australia (Brown 1941), and a limited number of crinoids are recorded from the Middle and Upper Palaeozoic of both eastern and western Australia.

Nevertheless some rare and interesting echinoderms have been found in Australia and undoubtedly many await discovery. Whitehouse (1941), described echinoderms from the Middle Cambrian or Thorntonia Station in north-western Queensland (lat 19°30′S., long. 138°55′E.) which were so unlike any previously known forms that he placed them in two new classes of a new sub-phylum—Haplozoa. They were associated with remains of cystoids, including "*Eocystis* (?)", which have not yet been described.

More recently Gill and Caster (1960) have described Silurian and Devonian carpoid echinoderms from Victoria, which are associated with "many other echinoderms—cystoids, blastoids, crinoids, machaerideans, starfish, and brittle stars".

The present paper records the occurrence of a new species of *Cheirocrinus* from the Ordovician of Western Australia. It is of considerable geological interest, even though at present it is represented by only one incomplete specimen, collected by Mr. D. Merrilees of the Western Australian Museum, Perth, Western Australia. It comes from the type-locality of the Emanuel Formation (Ordovician) in Emanuel Creek, lat. 18°39′S., long. 125°53′E. The approximate position is indicated in Figure 1, and is shown more accurately on the geological map by Guppy *et al.* (1958).

The discovery of a sequence of fossiliferous Ordovician rocks outcropping in the vicinity of Prices Creek over an area of about twelve square miles was first announced by Guppy and Öpik (1950) who described briefly the stratigraphy, structure and palaeontology of the sequence they named the Prices Creek Group. The occurrence was discussed later by Guppy *et al.* (1958) and by McWhae *et al.* (1958, pp. 28-29).

Fig. 1.

The Prices Creek Group consists of the (lower) Emanuel Formation and the (upper) Gap Creek Formation. A rich fauna obtained from both formations includes brachiopods, trilobites, gastropods and nautiloids which Guppy and Öpik recognised as ranging in age from Upper Ozarkian to Lower Trenton (Lower to Middle Ordovician) of the United States succession. The nautiloids have been described by Teichert and Glenister (1954). Earlier, Miss K. L. Prendergast (1935) had described a plectambonoid brachiopod, *Spanodonta hoskingae*, from beds now known as the Gap Creek Formation, which she mistakenly believed to come from the overlying Devonian. This brachiopod was recognised by Dr. G. A. Cooper of the U.S. National Museum, Washington, D.C. in 1946 (or earlier) as an Ordovician form (Browne 1952), but no details of its field-occurrence were known at the time.

The presence of *Cheirocrinus* in the Emanuel Formation confirms the previous evidence of the age of the formation, since the genus is known only from the Chazyan and Mohawkian (Trenton) of North America and from equivalent Lower and Middle Ordovician formations of Russia, Norway, Esthonia, Sweden, France, Portugal and Scotland. It has not hitherto been recorded from the Southern Hemisphere. (*See* Bassler & Moodey 1943). Unfortunately it is not known from which particular bed in the Emanuel Formation the specimen was derived.

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* Mrs. W. R. Browne, 363 Edgecliff Rd., Edgecliff, N.S.W.

I wish to thank Mr D. Merrilees for permission to examine this specimen.

### Systematic Description

| | |
|---|---|
| Phylum | ECHINODERMATA |
| Sub-Phylum | PELMATOZOA |
| Class | Cystoidea von Buch, 1844 |
| Order | Rhombifera Zittel, 1879 |
| Super-family | Glyptocystitida Bather, 1913 |
| Family | Cheirocrinidae Jaekel, 1899 |

Bather (*in* Lankester 1900, p. 58) used the old family name "Glyptocystidae" to include the genera *Glyptocystis*, *Cheirocrinus*, etc. In his independent work, which was in the press at the same time as Bather's, Jaekel (1899) proposed the family name "Chirocrinidae". Bather (1913) in his work on Girvan cystoids accepted this classification, but emended the name to Cheirocrinidae to agree with the spelling of *Cheirocrinus* Eichwald, 1856, with the explanation (p. 434)—"The name Cheirocrinidae has now been chosen instead of the old-established 'Glyptocystidae', so as to avoid confusion with other senses of the latter name, and in particular to render it possible for anyone to follow Prof. Jaekel in transferring '*Glyptocystis*' to the Callocystidae without having to alter any Family name". Bather (1913, p. 363) used "Glyptocystidae" as the name of a super-family, and this was modified to "Glyptocystitida" by Regnell (1945).

The family name Cheirocrinidae has been accepted by Bassler and Moodey (1943, p. 5) and by Bassler (1943, p. 669) and Regnell (1951).

The arrangement and orientation of the plates of the theca and the position of the pore-rhombs in this family have been the subjects of investigation by a number of writers. Bather (1900, p. 58) published a figure (reproduced in Fig. 2) showing the actual distribution of the pore-rhombs in all known members of the family, numbering the thecal plates which occur in five cycles, in the order 1 to 24 as shown in Figure 2, a scheme which he used again in his study of the Girvan fauna (Bather 1913).

Foerste (1920, p. 41), Bassler (1943), Sinclair (1948) and others have followed this scheme of nomenclature, although Regnell (1951) has preferred Jaekel's (1899) system of numbering the plates as basals, 1-4; infra-laterals, 1-5; laterals, 1-5; etc.

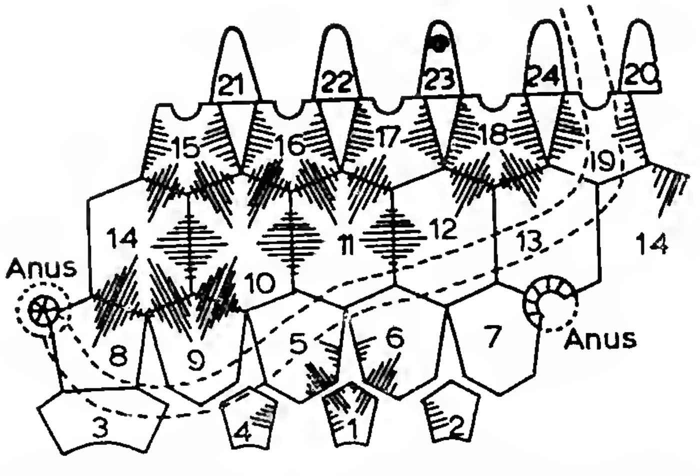

Fig. 2.—Diagrammatic sketch to show the actual distribution of the pore-rhombs in the Family Cheirocrinidae. (From Bather *in* Lankester 1900, p. 58, Fig. XX).

To avoid ambiguity for the Western Australian specimen and for easy comparison with similar specimens Bather's system is used in this paper.

### Genus **Cheirocrinus** Eichwald, 1856

Eichwald, E., 1856. Bull. Soc. Nat. Moscou 29 (1): 123. For Synonymy *See* Bassler and Moodey (1943, p. 142). Type-species: *Cyathocrinus penniger* Eichwald, 1842.

Eichwald's original definition (1856) is as follows:—"Diese Gattung zeichnet sich durch strahlig gerippte Schilder aus, die parallel den Rippen eine Reihe durch-gebrochner länglicher Poren für die Sauger zeigen und auf den Schulterschildern kurze gegliederte Hände tragen, fast wie der *Ichthyocrinus* Hall aus Nordamerika: der Kelch ist gestielt und die grossen *Cornuliten* scheinen zu ihm oder zum *Echinoencrinus giganteus* zu gehören, mit dem überhaupt diese Gattung viele Verwandtschaft zeigt".

The type-species, *Cheirocrinus penniger*, is known to occur in Russia and Esthonia. It has been studied by various workers including Kirk (1911), and Bather (1913, p. 436, Text-figure 41) who has given an analysis of the plates showing the positions of the pore-rhombs and the shapes of the individual plates as determined from the diagrams of Jaekel (1899).

Bassler and Moodey (1943, pp. 142-144) have recorded no less than 24 species now assigned to this genus and additional species have been described by Bassler (1943) and Regnell (1951). I have been unable to consult the monograph on *Cheirocrinus* foreshadowed by Sinclair (1948), but a study of the literature shows there is great variation in the characters of the thecae of these species and it seems probable that in future several distinct genera may be recognised. The Western Australian specimen falls within the range of the genus *Cheirocrinus* as understood at the present time.

### **Cheirocrinus merrileesi**, sp. nov.

(Fig. 3 (A, B, C), 4 and 5)

*Holotype.*—Western Australian Museum, Perth, Western Australia. Specimen No. 60.167.

*Locality.*—Emanuel Creek, Kimberley Division, 180 miles east-south-east of Derby, Western Australia.

*Formation.*—Emanuel Formation, Prices Creek Group. Ordovician. Collected by Mr D. Merrilees (22.VII.1960) on an expedition to the Fitzroy Trough. (*See* McKenzie 1961).

The specimen consists of the lower portion of a laterally compressed theca, of which twelve plates are preserved, comprising four infrabasals, five basals and three lateral plates, together with a few scattered anal plates and possibly portion of an ambulacrum adhering to one of the basal plates; the radiolateral and deltoid plates are missing and the column and brachioles are not preserved.

The specimen now measures about 18 mm in width, 6 mm to 7 mm in thickness and 21 mm in height. The complete thecal height was probably about 30 mm and the true width and

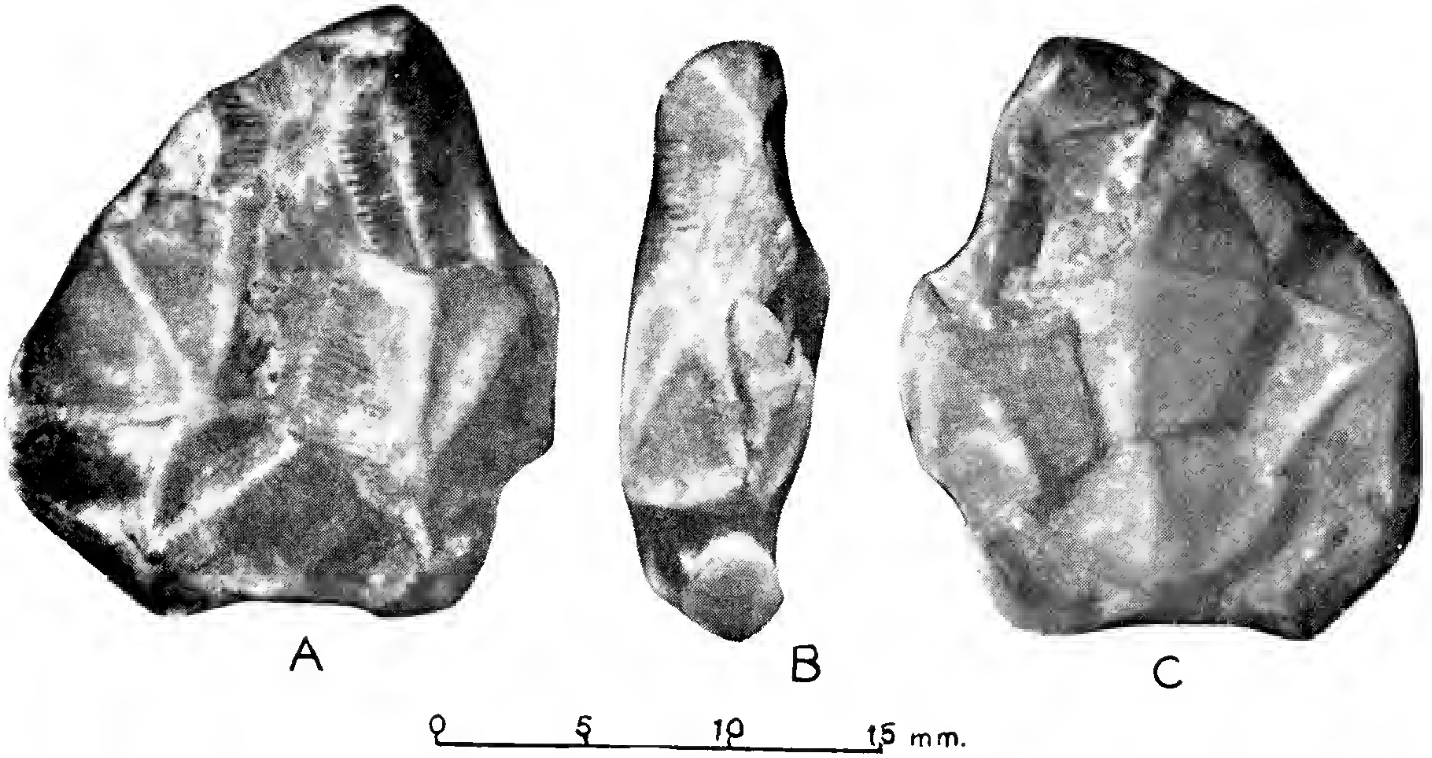

Fig. 3.—*Cheirocrinus merrileesi* sp. nov. Ordovician, Emanuel Formation, Emanuel Creek, Kimberley District, Western Australia. Holotype, Western Australian Museum, Perth, Western Australia Spec. No. 60.167. Photo I.A.B. A. Anterior, B. Left lateral and C. Posterior Views.

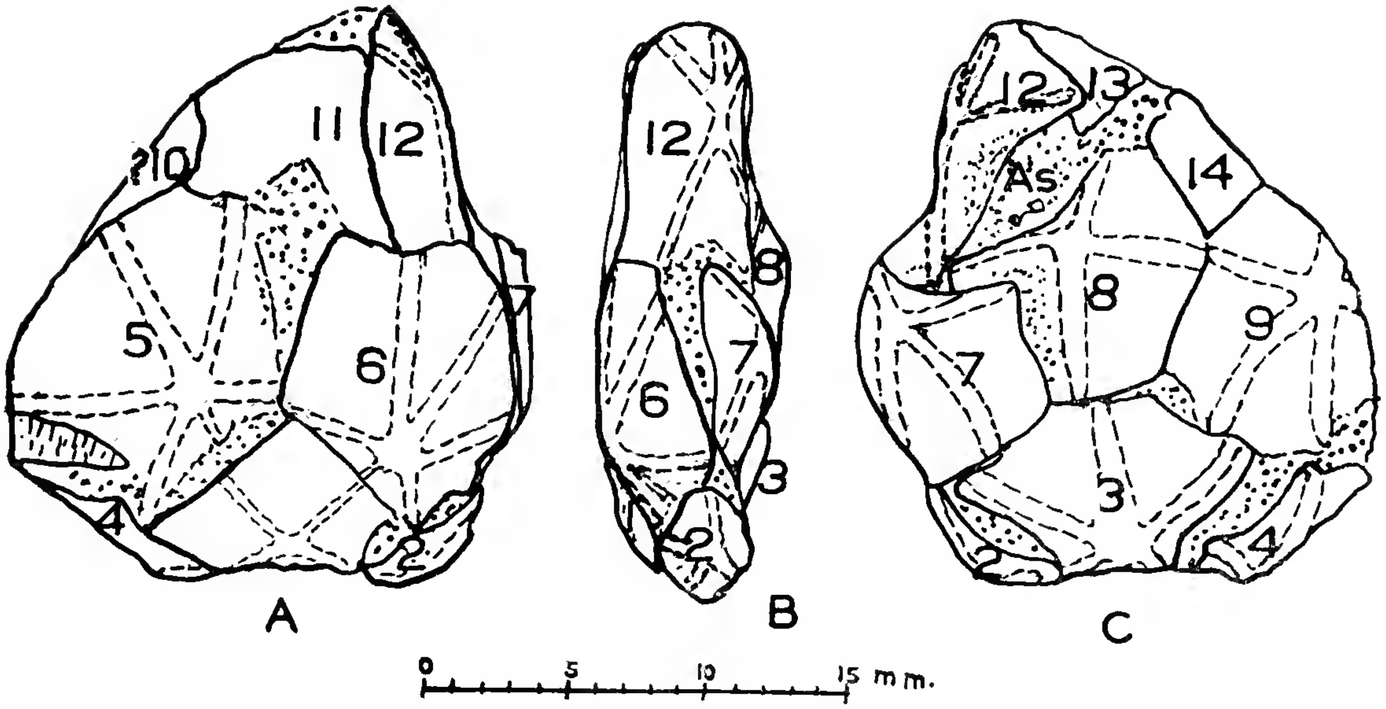

Fig. 4.—*Cheirocrinus merrileesi sp.* nov. Sketch of theca as shown in Fig. 3 to indicate identification of plates and position of radiating ridges.

thickness were rather greater than at present, since the plates have sprung apart along the sutures and some of the plates overlap, *e.g.* plates 1 and 6 overlap plate 5, and 7 overlaps part of 8. This displacement must have taken place during preservation, but except for plate 11, none of the individual plates appears to have suffered fracture or distortion.

Thus the complete theca was probably higher than wide, and considerably wider than thick, proportions which are characteristic of *Cheirocrinus* (Bather 1913, p. 435; Kirk 1911, p. 19).

The specimen is preserved in fine yellowish limestone, and the thecal plates are of crystalline calcite, the usual preservation of shells of fossil Echinodermata.

Each of the plates is thick, convex and has the well-marked radiating ridges characteristic of the genus, the centres of radiation usually being eccentric, as shown in the accompanying photograph (Fig. 3; A, B, and C) and corresponding diagram (Fig. 4: A, B, and C).

The positions of the ridges vary as indicated in Figures 3, 4 ,and 5. Sometimes they are normal to the middle of the sutures of adjacent plates and appear to have continued across the suture, *e.g.* from plates 3 to 7, 3 to 8, and 3 to 9: in plates 5 and 6 two of the ridges extend to the angles of the plates.

The analysis of the theca is shown in Figure 5.

No *column* is preserved but the scar for its insertion is clearly marked on the lower surface.

The *infra-basals*, plates 1 to 4, are variable in size: plates 2 and 4 are smallest; plate 1 is rhombohedral, modified at the lower edge for the insertion of the top of the column, while plate 3, the largest, is almost hexagonal, probably representing the fusion of two plates.

The *basals*, plates 5 to 9, are also variable in size; plates 5, 6 and 9 are hexagonal and plates 7 and 8 are modified for the anal area which is relatively large.

Of the lower *lateral plates* only plates 11, 12 and part of 14 remain. Plate 11 has been crushed inwards and its sutures with plates 5 and 6 are obscured. Plate 12 is folded about its vertical axis which is in the plane of compression of the theca, and its contact with the anal area is depressed. Only portion of plate 14, in contact with plates 8 and 9, is preserved. It was not considered advisable to remove more of the matrix on account of the risk of damage to the specimen.

No plates of the *fourth cycle*—plates 15 to 19—are preserved, but their existence must be presumed from the fact that the lower halves of pore-rhombs occur on plates 11 and 12, requiring plates 16, 17 and 18.

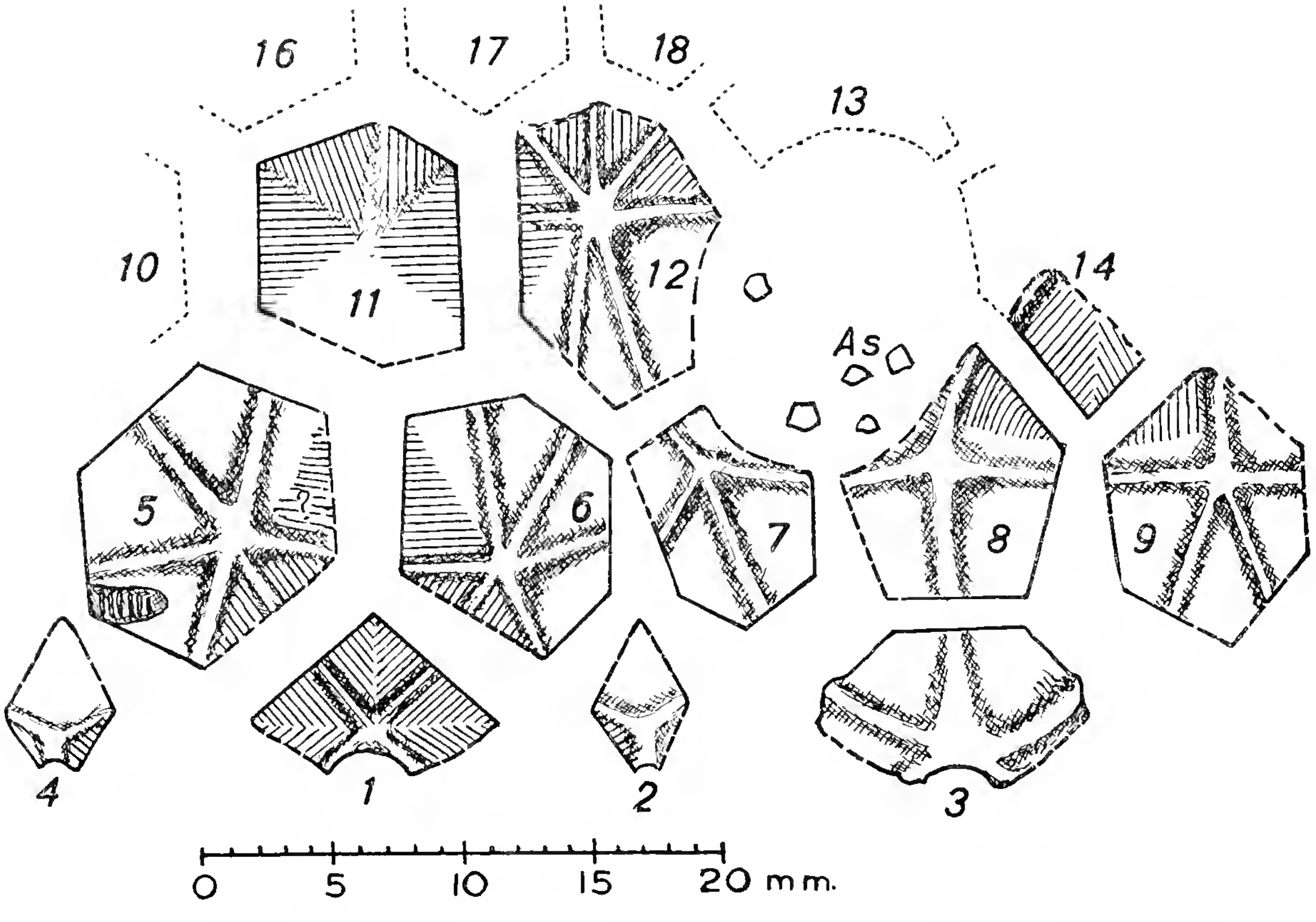

Fig. 5.—*Cheirocrinus merrileesi* sp. nov. Diagrammatic sketch to show structure and arrangement of the thecal plates, and the positions of the radiating ridges and pore-rhombs. Infra-basals 1-4, Basals 5-9, Lateral Plates 11, 12 and 14. Anal area, As.

There is a small water-worn piece of shelly material adhering to plate 5 which may be part of an ambulacral structure.

The arrangement of the pore-rhombs is shown in Figure 5. By comparison with Figure 2 it may be seen that it is in agreement with that of the Family Cheirocrinidae (Bather 1913). The pore-rhombs are all conjunct, the pore-slits passing uninterruptedly across the sutures. Rhombs 1/2 and 1/4 each have about 10 slits; 1/5 and 1/6 about 22 slits; rhomb 5/6 is abnormal in that the pore-slits, about 18 in number, form a triangular area on plate 6, such that the longest slit is not central, but at the end closest to plate 1; poor preservation prevents determination of all the pore-slits on plate 5.

A condition somewhat similar to that of plate 6 occurs on plates 8 and 9, where the longest slits are at one side, each against one of the radiating costae, but the slits pass directly across the sutures 8/14 and 9/14. Although plate 11 has been crushed inwards it bears its share of rhombs 11/?10, 11/?16, 11/?17 and 11/12.

A few scattered small plates indicate the anal area.

The remainder of the theca is lost.

*Remarks.—Cheirocrinus merrileesi* sp. nov. differs from all species of the related *Glyptocystites* in that plates 5 and 6 meet along a suture and are not separated by the upward extension of plate 1 to touch plate 11 (See Sinclair 1948, p. 310), and in this feature it differs also from *Cheirocrinus penniger* the type species of the genus (See Bather 1913, p. 436, Text-fig. 41).

Bather (1913) suggested a classification of the Cheirocrinidae based on the character of the rhombs, whether conjunct, disjunct or multidisjunct. *C. merrileesi* falls within his Group 1 ("Pectini-rhombs all, or at least on the base, conjunct".) in which he included only three species, *C. atavus* Jaekel, 1899, *C. giganteus* (Leuchtenberg, 1843) and *C. constrictus* Bather, 1913.

I have no specimens of described species of *Cheirocrinus* available for direct comparison, but to judge by the published descriptions and figures by Jaekel, Bather, Bassler, Sinclair and Regnell, the specimen from Western Australia differs from all other species in the arrangement of the plates and pore-rhombs, and therefore is regarded as a new species, which I have named *Cheirocrinus merrileesi* in honour of Mr. D. Merrilees.

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# 3.—Description of a new Stonefish of the family Synanceidae from Western Australia

By R. J. McKay*

*Manuscript received—18th June, 1963*

A new species of the genus *Inimicus*, belonging to the family Synanceidae from Western Australia is described and compared with other members of the genus. Notes on the ecology including an account of the severity of the sting of the new species are included.

## Introduction

During the years 1958, 1960 and 1962 the Western Australian Fisheries Department obtained a large collection of fishes as a result of the resource surveys carried out by the research vessels *Lancelin* and *Peron*. The majority of the fish were collected in the Shark Bay and Exmouth Gulf areas. Over the past five years, the author has devoted much of his spare time to the study of certain groups of this collection.

The Western Australian coastline is poorly known ichthyologically, and therefore it is not surprising to find that much of the collected material is not recorded from the State, and that a few species are found to be new.

This paper presents the description of one of the species considered to be new. The opportunity has also been taken to record information on the ecology of the species.

Genus **Inimicus** Jordan and Starks, 1904
Genotype *Pelor japonicum* Cuvier, 1829

**Inimicus cirrhosus**† species nova
*Inimicus didactylus;* Mees 1960, p. 19.

### *Differential diagnosis*

Differs from all others of the genus in the possession of yellow spots on the inner surface of the pectoral fin.

### *Description*

The description is based on the holotype and fifteen paratypes. The counts and measurements within the parenthesis are those of the paratypes. D. III XIV, 9 (III XIII-XV, 8-10). A. II, 12. (II-III, 12-13). P. 1, 6, 3 + 2   12 (1 — 2, 5 — 6, 3 — 4 + 2 — 3). V. I, 5. (I, 5). C. 2, 9, 3   14 (2 — 3, 8 — 9, 3 — 4   13 — 14). Gill rakers 2 + 7.

Head 2.9 (2.7 — 3.2); depth of body 3.4 (2.6 — 4.0); pectoral fin 2.8 (2.5 — 3.1), all in standard length. Eye 5.4 (5.0 — 7.0) in head, 1.5 (1.4 — 2.1) in interorbital, 2.6 (2.4 — 3.3) in snout.

Interorbital 1.8 (1.4 — 1.8) in snout, 3.6 (3.0 — 4.0) in head. Snout 2.0 (2.0 — 2.5) in head. Longest dorsal spine 1.5 (about 1.5) in head.

Head about as wide as long, snout greater than postorbital part of head, and almost half length of head. Head grotesquely shaped, depressed. Bony orbits elevated and prominent, with 2 or 3 low blunt knobs superiorly. A groove immediately below eye, preorbital pits shallow, interorbital space deeply concave with transverse ridge branching on to orbits at rear. A deep transverse depression behind eyes, nuchal and post-temporal spines developed. One anterior and two posterior spines on suborbital stay. Coronal ridges on snout more or less developed in smaller examples, well developed in larger specimens.

Preorbital with two blunt spines on upper surface, ending in a sharp spine normally covered with skin. Nostrils low and tubular; anterior pair situated on each side of nasal hump or protuberance; posterior pair situated behind this protuberance. Preopercle with 4 spines; lower 2 blunt and scarcely worthy of being called spines; upper 2 sharp, superior spine with a ridge preceding. Opercle terminating in a fleshy flap; upper portion of opercle with 2 well developed radiating ridges, uppermost ending in a spine.

Mouth small, oblique; lower jaw projecting, with a small symphysial knob at tip. Maxillary with posterior end expanded; width posteriorly almost equal to eye diameter. Maxilla ends well before eye. Mandibulary ramus expanded posteriorly.

Teeth small, sharp, and conical; 4-5 series in both jaws, fewer posteriorly; similar teeth in 4-5 series on vomer. Palatines toothless. Tongue triangular, free at tip, upper surface smooth generally with few low tubercles near margin.

Gill rakers 1 — 3 + 7 — 8, low, knoblike and intensely spiniform.

Branchiostegal rays 7. Gill membranes united to isthmus but not broadly so.

Body elongate, little compressed, tapering posteriorly almost in a straight line along dorsal surface from 4th or 5th dorsal spine.

The 3 anterior dorsal spines almost detached from the rest of fin, with membrane almost to their tips. Remaining 13-15 spines, except last 1 or 2, have interspinous membrane low. Dorsal spines sharp, slender and strong, grooved at tips, skin reaches tips of spines in most examples. All spines except first 3 and last 3, almost uniform height. Dorsal rays decrease in length posteriorly, last ray connected to caudal peduncle by membrane, only tip free. Anal fin low, spines sharp but embedded in thick skin. Tips of anal rays slightly thickened, free for about one-third of their length, last 3 with membrane to tips.

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† From the Greek kirrhos, yellow.

Pectoral fin large, extending well past origin of anal. First 1 or 2 and last 5 or 6 pectoral rays simple, intermediate ones branched. Lower 2 pectoral rays free, for the most part; generally curved, thickened slightly, and almost equal in length. Length of ventral fin almost equal to that of head, adnate to belly with free tips of the rays reaching well beyond anus.

Caudal fin rounded, length almost equal to that of head, outermost 2 or 3 rays normally simple. Caudal peduncle less than interorbital measurement.

Body and head without scales. Skin loose, with dermal flaps, filaments, skinny tentacles and branched appendages, especially on head, chin, mandibles, margins of preopercle and pectoral fin, and upper surfaces of sides and back. Well developed branched dermal appendages on each side of chin, placed low on preopercle margin.

A somewhat obscure lateral line present with 12 to 13 pores along its length. A few pores above lateral line near dorsal surface; all pores have small mostly branched dermal appendages.

### *Colour*

Body and head generally brownish, densely mottled with lighter and darker diffuse blotches and variable marblings. Holotype deep brown with areas of lighter brown and patches of grey-white near 1st, 4th, 5th and 10th to 15th dorsal spines, extending below lateral line; a pale diffuse bar through soft dorsal fin. Lower sides and belly with numerous scattered light and dark flecks and diffuse blotches. Ventrals uniform brown. Caudal with 2 vague narrow whitish cross-bars or two rows of white spots (in life, yellow).

**Pectoral fin dark brown, almost black with indistinct pale cross-bars and variable blotches on outer surface. Inner surface dark brown to blackish, with 20 to 35 white (in life bright yellow) spots of indefinite shape. In larger examples the yellow spots are more diffuse and frequently in the form of ocelli. (Fig. 1a).**

Base of pectoral fin, and lower sides of belly above ventral fins, pale with brown flecks and indistinct marblings.

One paratype has body yellowish with scattered brown spots on body and a few dark spots on head; dorsal fin plain yellow. Caudal brownish with scattered dark brown and yellow spots. Lower portions of body brownish with some scattered dark spots. Ventrals brownish with a few scattered darker spots. Outer surface of pectoral fin yellow with scattered dark brown spots. Inner surface of pectoral fin brownish with yellow spots, about eye diameter in size: 2 to 3 rows of smaller dark brown spots near margin of fin, and a few scattered dark spots on fin, especially near base.

### *Material Examined*

Unless otherwise stated, all Western Australian Museum material was taken by trawl net on the State Fisheries Research Vessels *Lancelin* and *Peron*, collected by the author. Western Australian Museum and Australian Museum registered material is abbreviated WAM and AM respectively.

I. cirrhosus

Holotype.—WAM P 4980 164 mm total length, 125 mm standard length, approx. 9 miles north of Cape Peron Flats, Shark Bay, 1.X.1960.

Paratypes.—WAM P 4983 198 mm t.l., 155 mm s.l., Exmouth Gulf 14.XI.1960; P 4987 322 mm t.l., 256 mm s.l., Rat Island, Abrolhos Is., 2.III.1963 hand spear whilst diving in 9 fathoms; 13 specimens from Shark Bay collected between 23.V.1960 and 27.X.1960 WAM P 4981, P4982,

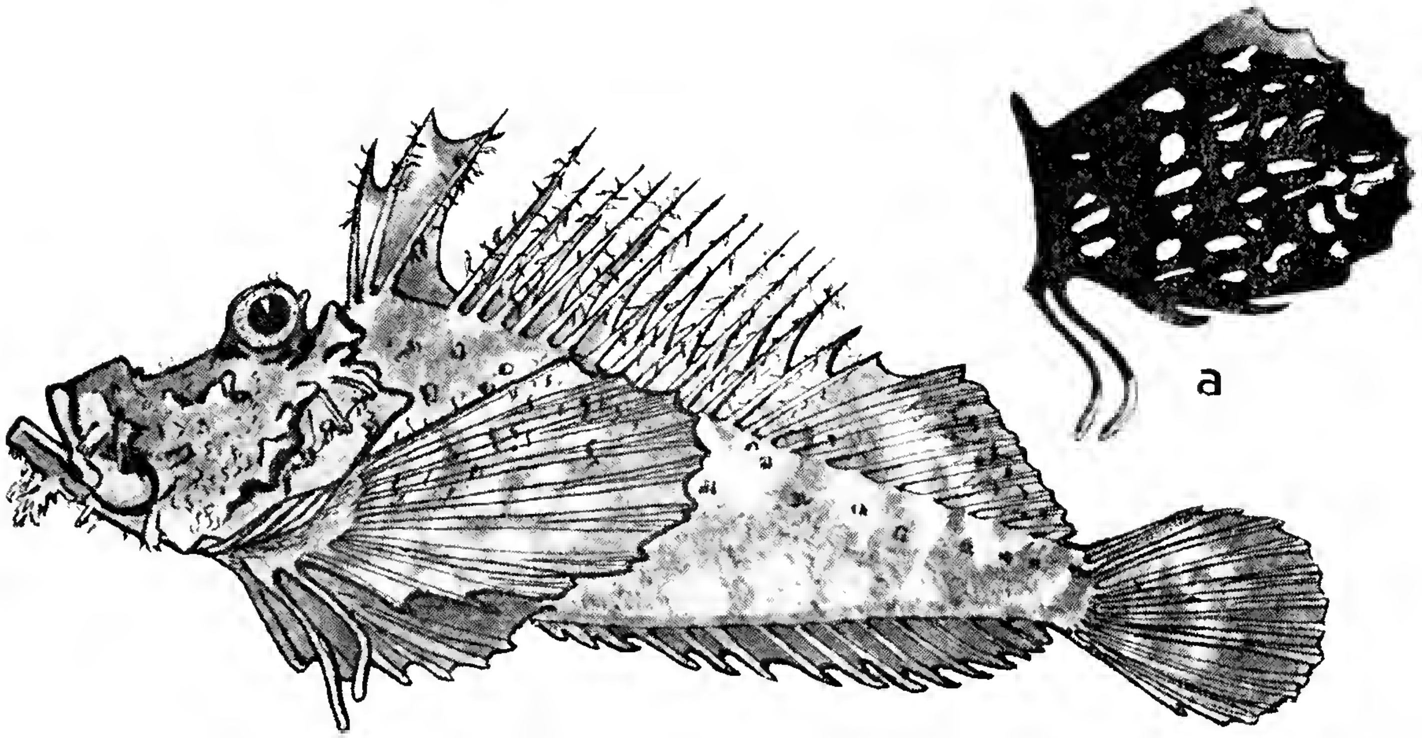

Fig. 1. *Inimicus cirrhosus*. a. Inner surface of pectoral fin showing markings.

P 4984, P 4985, P 4986 and P 4988 to P 4995 inclusive, range of measurements 75 to 257 mm t.l., 56 to 203 mm s.l.

Other species

*I. didactylus* (Pallas) AM 1B.4439 and 1.1499, 2 specimens.

*I. japonicus* (Cuvier) AM 1.13702, 1 specimen.

*I. barbatus* (De Vis) AM 1A.4782, 1A.6137, 1A.6671, 1A.6672, 1.14039, 1.10933 and 1B.1716, 7 specimens.

### *Distribution*

Known from Exmouth Gulf, Abrolhos Islands and the type locality, Shark Bay.

### *Comparison with Other Species*

*Inimicus cirrhosus* appears closest to *I. didactylus* and *I. barbatus*, their structural details and body proportions being very similar.

On examining the two specimens of *I. didactylus* at the Australian Museum, it was found, as McCulloch (1916, p. 197) noted, that the coloration and markings of the inner surface of the pectoral fin agreed with Bleeker's (1874, pl. IV, figs. 1-1A. 1878, pl. CCCCXIV, figs. 5-5a) plates of this species.

The specimens of *I. barbatus* have the coloration and markings of the inner surface of the pectoral fin as McCulloch (1916, pl. LVIII) figured.

Bleeker (1874, p. 1) and McCulloch (1916) have remarked on the importance of the coloration and markings on the inner surface of the pectoral fin in determining species of *Inimicus* as these are consistent within a species. This is true for *I. cirrhosus*, as over 200 specimens were checked from Shark Bay and Exmouth Gulf during 1958, 1960, and 1962.

The 2 specimens of *I. didactylus* examined had the eye equal to the interorbital space, and in *I. cirrhosus*, the eye in interorbital space ranged from 1.4 to 2.1. Herre (1951, p. 472) records the eyes as being about a diameter apart in Philippine specimens of 48 to 128 mm in length. Fowler (1927, p. 288) gives eye as 2 in interorbital in a Philippine specimen of 183 mm, while Day (1878, p. 161) gives eye as 1-1¼ apart in a specimen of 5½ inches from the Andaman Islands. McCulloch (1916) records variation in interorbital space for *I. barbatus*, being narrower in smaller examples; this is generally so in *I. cirrhosus* (see Table 1).

Bleeker (1878, pl. CCCCXVI, figs. 3-3a) shows the pectoral fin markings of *I. cuvieri* (Gray) and on pl. CCCCXIII, figs. 1-1a, the pectoral fin markings of *I. brachyrhynchus* (Bleeker). The pectoral fin markings of *I. maculatus* ( *I. didactylus*), and *I. filamentosus* (Cuvier) were also figured. Published descriptions by Günther (1860, p. 150), Herre (1951, p. 470 and p. 473), and Fowler (1927, p. 289; 1928, p. 299) agree with Bleeker's plates.

The specimen of *I. japonicus* examined has the eye 2.0 in interorbital, snout 2.7 in head, and the postorbital part of head (25 mm) is greater than the snout (19 mm). Günther (1860, p. 151), gives eye as 2.5 in interorbital, and an anal ray count of 9, for this species, while Tanaka (1914, p. 248) records counts of 7 dorsal and 9 anal rays in a specimen of 220 mm, and gives snout as 2.5 in head.

Smith (1958, p. 276) records D. as III XII, 8, A. III, 8, "and pectoral and caudal with middle parts light" for *I. filamentosus*. Fowler (1938, p. 86) gives coloration of pectoral fin of *I. bifilis* (Fowler) as having "broad white subbasal band, adjoining blackish area over branched rays and another terminally; lower detached rays with dark spots". *I. bifilis* has a dorsal count of XVII, 8, and an anal count of 13.

*I. caledonicus* (Sauvage) has a dorsal ray count of 7, and a total anal count of 12. (Fowler 1928, p. 299. (after Sauvage)).

### *Variation in Pectoral Rays*

Paratype WAM P 4994 has 3 free pectoral rays on the right hand fin, the first 2 are joined for half their length; the left hand pectoral fin has the normal 2. The joined pectoral rays in this specimen number 9 instead of the usual 10.

**TABLE I**

Measurements in mm and fin ray counts of *I. cirrhosus*

| | P.4980 | P.4981 | P.4982 | P.4983 | P.4984 | P.4985 | P.4986 | P.4987 | P.4988 | P.4989 | P.4990 | P.4991 | P.4992 | P.4993 | P.4994 | P.4995 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total length | 164 | 191 | 220 | 198 | 257 | 209 | 238 | 322 | 98 | 75 | 133 | 116 | 99 | 121 | 155 | 136 |
| Standard length | 125 | 150 | 180 | 155 | 203 | 167 | 190 | 256 | 75 | 56 | 106 | 90 | 77 | 93 | 119 | 106 |
| Length of head | 43 | 52 | 62 | 52 | 76 | 54 | 60 | 88 | 25 | 21 | 33 | 31 | 25 | 32 | 42 | 37 |
| Length of snout | 21 | 25 | 29 | 23 | 34 | 26 | 28 | 30 | 12 | 10 | 16 | 14 | 12 | 14 | 20 | 15 |
| Diameter of eye | 8 | 9 | 10 | 9 | 10 | 9 | 11 | 13 | 4 | 4 | 6 | 5 | 5 | 5 | 6 | 6 |
| Interorbital | 12 | 14 | 18 | 13 | 19 | 16 | 17 | 27 | 7 | 6 | 11 | 8 | 7 | 10 | 11 | 10 |
| Greatest body depth | 37 | 43 | 58 | 48 | 79 | 50 | 56 | 81 | 20 | 16 | 32 | 24 | 23 | 23 | 23 | 29 |
| Length of pectoral fin | 45 | 49 | 60 | 53 | 70 | 59 | 62 | 83 | 30 | 21 | 37 | 32 | 26 | 30 | 45 | 41 |
| Length of upper free pectoral ray | 39 | 30 | 35 | 28 | 41 | 32 | 39 | 57 | 15 | 13 | 20 | 16 | 16 | 18 | 17 | 23 |
| Length of lower free pectoral ray | 40 | 32 | 32 | 31 | 13 | 31 | 39 | 62 | 16 | 13 | 23 | 19 | 16 | 17 | 19 | 23 |
| Soft dorsal base | 32 | 37 | 47 | 40 | 50 | 47 | 39 | 67 | 20 | 14 | 26 | 22 | 21 | 20 | 28 | 30 |
| Anal base | 54 | 61 | 78 | 69 | 93 | 80 | 84 | 114 | 35 | 27 | 50 | 37 | 38 | 44 | 53 | 52 |
| Ventral base | 35 | 37 | 45 | 42 | 61 | 47 | 49 | 71 | 20 | 16 | 27 | 26 | 22 | 25 | 38 | 33 |
| Depth of caudal peduncle | 11 | 11 | 13 | 12 | 12 | 12 | 14 | 20 | 6 | 5 | 8 | 8 | 6 | 7 | 8 | 9 |
| No. of dorsal rays | 9 | 9 | 9 | 9 | 8 | 10 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 8 | 8 | 9 |
| No. of anal rays | 12 | 12 | 12 | 12 | 12 | 13 | 13 | 12 | 12 | 13 | 12 | 12 | 12 | 12 | 12 | 12 |
| No. of caudal rays | 14 | 13 | 13 | 14 | 13 | 14 | 14 | 14 | 14 | 14 | 14 | 13 | 14 | 14 | 14 | 14 |

Paratypes WAM P 4988 and P 4989 have the two uppermost pectoral rays filamentous at their tips, the rays extend 8 mm and 12 mm from the tip of the pectoral fin respectively. Paratype WAM P 4922 has only the upper pectoral ray filamentous; this ray extends 18 mm from the pectoral fin membrane, 7 mm from the tip of the pectoral fin. This condition apparently exists in the juveniles as these 3 paratypes measure 75, 56, 77 mm in s.l. respectively.

In view of these observations of the juvenile characters of *I. cirrhosus*, it is possible that some "species" with similar characters may be juveniles of other species. The type of *I. bifilis* from the Philippines measures only 57 mm in length and Fowler remarks "Greatly like *Inimicus filamentosus*, but only the uppermost pectoral ray ending in a filament which reaches well beyond the depressed pectoral fin". This could be a juvenile condition of perhaps *I. cuvieri* or *I. didactylus* which have been recorded from the Philippines by Herre (1953, p. 576).

### *General Biology and Ecology*

*I. cirrhosus* was found to be a sluggish, bottom-dwelling marine form inhabiting open, sandy, or silty types of substrates. Inside Shark Bay, it has a wide distribution and is commonly taken on prawn trawling grounds, often in association with Scallops *Amusium balloti* Bernardi. Two or 3 per haul are not uncommon. The greatest number recorded inside Shark Bay during 1962 was 14 during a 45-minute trawl.

During 1961, F.R.V. *Peron* used a temperature-chlorinity conductivity meter, and specimens of *I. cirrhosus* were collected in salinities ranging from 35.7‰ to 44.9‰, and temperatures from 18.2°c. to 26.4°c. The depths recorded on the echo sounder were between 7 and 12 fathoms.

Partly digested fish were found in the stomachs of 2 specimens; these were identified as *Monacanthus sp.* and *Equula fasciata* (Lacepede).

A near-ripe female, t.l. 215 mm, was trawled inside Exmouth Gulf early in October, 1958. One ripening female t.l. 220 mm trawled inside Shark Bay early in February, 1962, had ova 0.8 mm in diameter, and 3 females, t.l. 210 to 265 mm were found to be spent during May, 1962.

Like other members of the family *Synanceidae*, they are reluctant to move when approached, and lie quite motionless, even when spilled from the trawl net on the deck of the vessel. One was taken underwater and the fish made no attempt to move, but quickly spread the dorsal spines to afford protection from most directions. The pectoral fins were extended to show the markings on their inner surface. The fish was not easily recognised in its natural surroundings, as it was covered to some extent by fine sand, and appeared quite hirsute due to the dense covering of demal cirri and appendages.

### *Notes on Severity of Sting*

This species is capable of inflicting an extremely agonising wound. The following notes were made early in October, 1960, after the author was stung on the thumb. The pain was immediate and intense, the wound bled very freely for a few minutes then ceased. Bleeding was difficult to restart. Pain became rapidly unbearable.

1145 hrs. While sorting a trayful of fish emptied from trawl 31, left thumb deeply penetrated by dorsal spine of *Inimicus*. Bleeding freely.

1150 hrs. Bleeding stopped.

1155 hrs. Thumb swollen, area around wound becoming grey-blue in colour, extremities of fingers becoming very painful, pain in thumb almost unbearable. Elbow and shoulder now aching.

12 midnight. Sweating profusely, thumb and hand swollen, wrist very stiff, area around wound bluish, throat and mouth dry.

0005 hrs. Became delirious, do not remember much, but can recollect throwing myself about the cabin in fearful pain. Crew members restrained my movements for the next 30 minutes, during which I was screaming and complaining of pains around chest and neck.

0045 hrs. Regained full consciousness, the pain in arm and shoulder very agonising.

0115 hrs. Hand and thumb immersed in hot water and sedatives taken.

0200 hrs. Pain still present but greatly diminished.

Thumb remained stiff and swollen for four days, but the pain had subsided 12 hours after encounter. Bathing the wound with hot water greatly reduced pain, but when the water became cool enough to be comfortably borne, the pain returned. A tourniquet was not applied.

Stings by fishes such as Scorpaenids *Paracentropogon vespa* (Ogilby), *Apistus carinatus* (Bloch) and *Minous monodactylus* (Bloch & Schneider), and a stingray *Amphotistius kuhlii* (Müller & Henle) were quite common on board prawn trawlers operating inside Shark Bay. From personal experience, the sting of *I. cirrhosus* is considerably more painful than any of these species.

### Acknowledgments

I wish to record my appreciation to those persons who assisted me in my studies and gave much helpful advice in the preparation of this paper: Dr. G. F. Mees, of the Western Australian Museum and Mr. A. J. Fraser, Director of the Western Australian Fisheries Department read the manuscript; Mr. G. P. Whitley, of the Australian Museum, gave helpful advice and assistance while I studied fishes under his care; the skipper, Mr. H. C. W. Piesse, and crew of the Fisheries Research Vessels *Lancelin* and *Peron*, assisted in collecting fishes during trawling investigations and administered assistance during the ordeal of the *Inimicus* sting.

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# 4.—Association of Larger and Planktonic Foraminifera in single samples from Middle Miocene sediments, Guadalcanal, Solomon Islands, south-west Pacific

By P. J. Coleman[*] and R. A. McTavish[†]

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Single samples from Miocene sediments in north-central Guadalcanal, Solomon Islands, contain both larger foraminifera and planktonic species of the *Sphaeroidinellopsis seminulina* fauna. This association was contemporaneous during Middle Miocene (Vindobonian) time. *Lepidocyclina ("Multilepidina") suvaensis* (Whipple), *Lepidocyclina (Nephrolepidina) japonica* Yabe, *Cycloclypeus (Katacycloclypeus) martini* Van der Vlerk and *Miogypsina polymorpha* (Rutten) survived well into the Vindobonian, at least in this part of the Indo-Pacific region.

## Introduction

Until a few years ago the age-determination and correlation of Tertiary sediments by means of their foraminifera was based principally on the so-called larger foraminifera with but minor support from the smaller benthonic forms. Over recent years, however, the use of planktonic foraminifera for this purpose has become increasingly common, as might have been expected on purely theoretical grounds, and has been justified in practice. Studies of the planktonic foraminifera, however, are usually made independent of those on larger forms. There are reasons for this—these two groups require different methods of study; more important, sediments containing abundant planktonic species of foraminifera are usually barren of the larger forms, and vice versa, a reflection of their different life environments. This kind of mutual exclusiveness, however, carries with it the risk that age-determinations and correlations based on the one group will differ from those based on the other (see Cole, Todd and Johnson 1960; Glaessner 1960)—a situation which has been common enough in applied palaeontology. The chance of such conflict can be reduced if a sufficient number of mutual occurrences, of stratigraphically defined normal associations, can be established. This paper attempts to provide one such link between larger and planktonic foraminifera which will be applicable to Miocene foraminiferal faunas, at least in the Indo-Pacific region.

Larger foraminifera of the Solomon Islands have been described by Coleman (1963*a*), and the planktonic forms by McTavish (1963). In the Solomon Islands sediments, as elsewhere, the two groups are not usually found together in the same formation much less in the same sample. There are two localities, however, in which both have been found together in single samples and a third where samples bearing planktonic forms are only 50 feet stratigraphically above those with larger foraminifera, in strata making up an uninterrupted succession of rapidly-deposited sediments. The first of these, from Middle Miocene sediments in the Tangaraisu River, north-central Guadalcanal, provided the material for this paper. The others are in Aquitanian (Tertiary upper 'e') sediments on San Cristoval and San Jorge, respectively, where there are associations of *Eulepidina ephippioides, Spiroclypeus leupoldi, Heterostegina borneensis, Miogypsina thecideaeformis, Miogypsinoides dehaartii* and *Cycloclypeus eidae* with *Globigerina bollii, G. (Globigerinita) dissimilis, G. (G) unicava, Globigerinoides quadrilobatus, Globoquadrina dehiscens* and *G. venezuelana*; these Aquitanian associations are to be described in another paper.

## Stratigraphical Background

A traverse along the middle and upper reaches of the Tangaraisu River gives the most complete and least faulted section yet found in north-central Guadalcanal, although faults are still frequent. The sedimentary part of this section was closely sampled by Coleman in 1961. Three of the samples contained both planktonic and larger and small benthonic species of foraminifera.

The geology of the general area was described by Coleman (1960). Figure 1 shows a map and section of the Tangaraisu River area, based on additional fieldwork, and also a general map of Guadalcanal taken, with slight modification, from the first regional geological map of the British Solomon Islands (Coleman 1963*b*; Coleman *et. al. 1963*). The Miocene sedimentary succession begins with the Betilonga Limestone, a fringing-reef formation about 1200 feet thick. At the base it has a foraminiferal fauna indicating an Aquitanian age, with *Eulepidina, Spiroclypeus, Miogypsinoides dehaartii, Heterostegina borneensis* and *Cycloclypeus eidae*. At the top it becomes finer grained, lacks reef characteristics, and grades into the overlying Tina Calcarenite which has a fauna more typically Burdigalian. It includes *Lepidocyclina (Nephrolepidina) martini, L. (N.) radiata, L. (N.) ferreroi* and *Miogypsina polymorpha*. The Tina Calcarenite is a medium to fine-grained sediment, coarsely bedded with a minor terrigenous content of unaltered ferromagnesian and feld-

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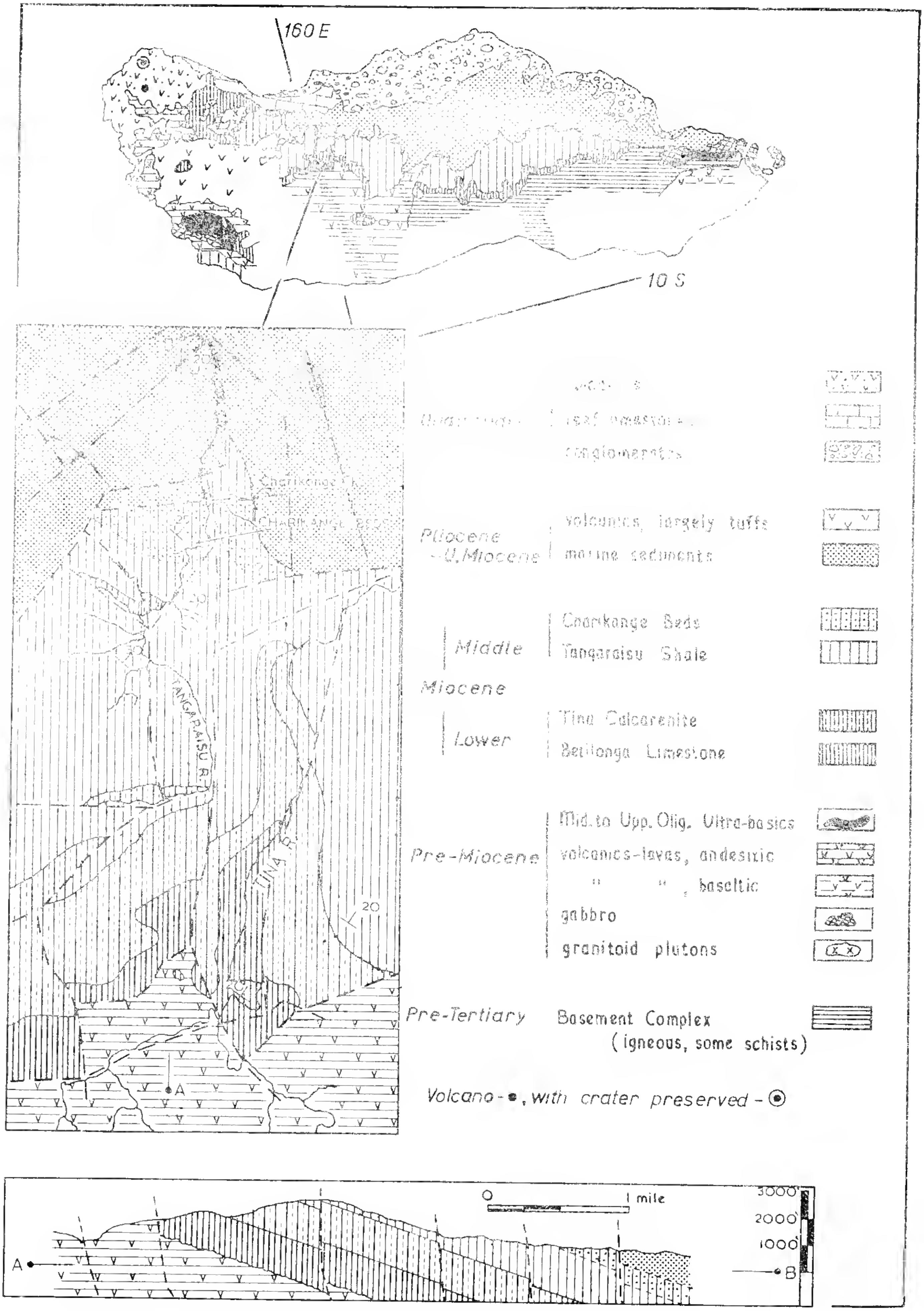


Fig. 1.—Geology of the Tangaraisu River area with reference to a generalized geological map of Guadalcanal, British Solomon Islands.

spathic grains derived from the andesitic basement; it is about 1,400 feet thick. It contains abundant planktonic as well as larger foraminifera but the former could not be extracted for indentification. Towards the top it is marked by shaley partings which, over a short vertical distance, become predominant to form the base of the Tangaraisu Shale. This is at least 2,000 feet thick, is argillaceous and finely bedded for the most part, but includes many bands of fine-grained lithic volcanic sandstone and occasional conglomerate beds. Near the top of the formation the sediment becomes generally coarse-grained to form the Charikange Beds, a minor unit about 500 feet thick. These beds are banded but poorly bedded, show a good deal of lithological variation and include intraformational structures such as cross-bedding, graded bedding, minor slump folds and displaced small blocks. The banding is due to alternations in grain size and in the proportion of shell fragments. The samples to be described come from near the base of the Charikange Beds. The remainder of the sedimentary succession is made up of the Toni Beds and Mt. Austen Beds, of Pliocene age, and the Honiara Beds of Quaternary age. These consist of organogenic and volcanic or volcanically-derived sediments.

In this part of Guadalcanal, therefore, the sedimentary sequence from basement to the top of the Charikange Beds is about 4,700 feet thick; it shows a regular progression from reef to deeper water sediments with increasing terrigenous content and without evidence of a sedimentary hiatus. The younger sediments were deposited rapidly in fault-bounded troughs and derived from an andesitic terrain which was being uplifted and eroded rapidly. The Charikange Beds mark a time of acceleration in this action.

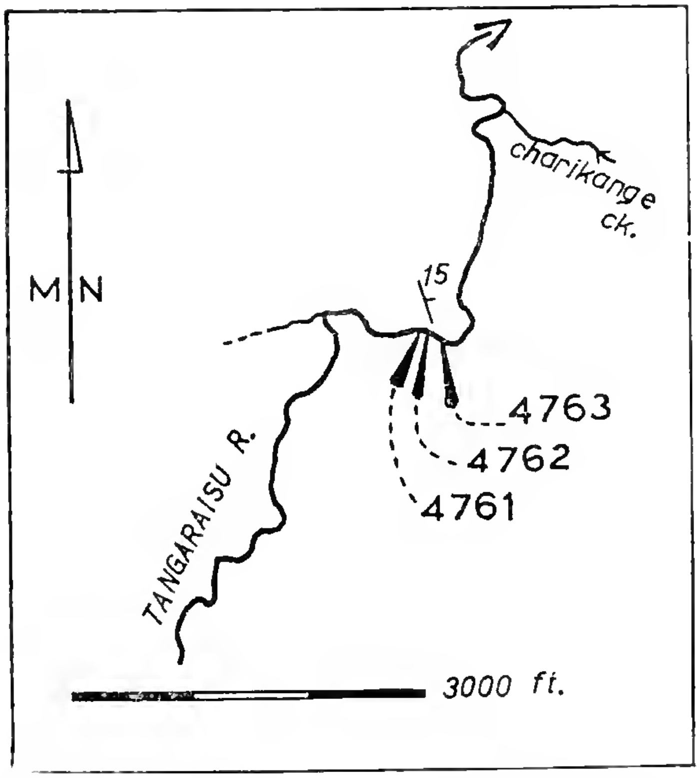


Fig. 2.—Locality map of samples 4761, 4762 and 4763 from the Charikange Beds, Tangaraisu River, north-central Guadalcanal.

**Description of the Samples**

The samples have British Solomon Islands Geological Survey collection numbers 4761, 4762, and 4763, respectively; splits of them have been retained by that Survey. They were taken from an unfaulted cliff face, at about 80 feet vertical intervals, approximately 550 yards upstream from the junction of Charikange Creek and the Tangaraisu River. The locality is shown in Figure 2. Its co-ordinates on the 1,000 metre Southern New Guinea Zone British Metric Grid, Bessel Spheroid, are 4102650/810620, eastings first.

The grain size in the samples ranges from interstitial clay to rare rock fragments several centimetres across. The larger grains are usually of the order of 2-5 mm across and include larger foraminifera, shell fragments, fragments of andesite and occasional basaltic rocks (mostly lava types), dioritic rocks and, especially important, eroded fragments of Tina Calcarenite and Betilonga Limestone; of these two, the latter is the most frequently represented. The rock fragments are subangular to angular. The mineral content consists of organic calcite, hornblende, plagioclase (andesine-labradorite), hypersthene, epidote, clinopyroxene, chlorite, mica and quartz in that order of abundance. The grains are fresh and many are euhedral. Organic calcite varies from 30% to 60% of the total weight. The cement is calcareous, usually crystalline, but it may be in the form of clay. Size analyses were made of two of the samples, 4761 and 4763. The former had a tenacious calcite cement and could be disaggregated only after treatment with hydrochloric acid. The sample was a large block which included part of a coarse band and part of an underlying fine band. Each portion was analysed separately, the coarse part being 4761A, the fine part 4761B. Sample 4763 was broken down with considerable difficulty, and to judge the effect on the sorting of the foraminifera and other organic calcite, it was examined in its original state (4763A) and after treatment with hydrochloric acid (4763B). The resultant distribution curves are shown in Figure 3. The coarse part of 4761 is poorly sorted whereas the fine part is well sorted. Sample 4763 is moderately sorted although the acid-treated part (4763B) shows that the removal of organic calcite improves the sorting. This effect is confirmed by qualitative examination of the larger foraminifera present in the untreated part of the sample; they range in random fashion from clearly immature small specimens, to large mature specimens. The results of these analyses are not very significant, but they do support the idea, deduced from a variety of other evidence, especially field evidence, that the Charikange Beds were deposited under swiftly varying conditions and that they are turbidites, at least in part. A more formal attempt to determine the processes of deposition of these beds, using the CM patterns of Passega (1957), had to be abandoned because most of the samples could not be broken down without the use of hydrochloric acid, and this destroyed the large and vital fraction made up of transported coarse shell fragments and other organic grains.

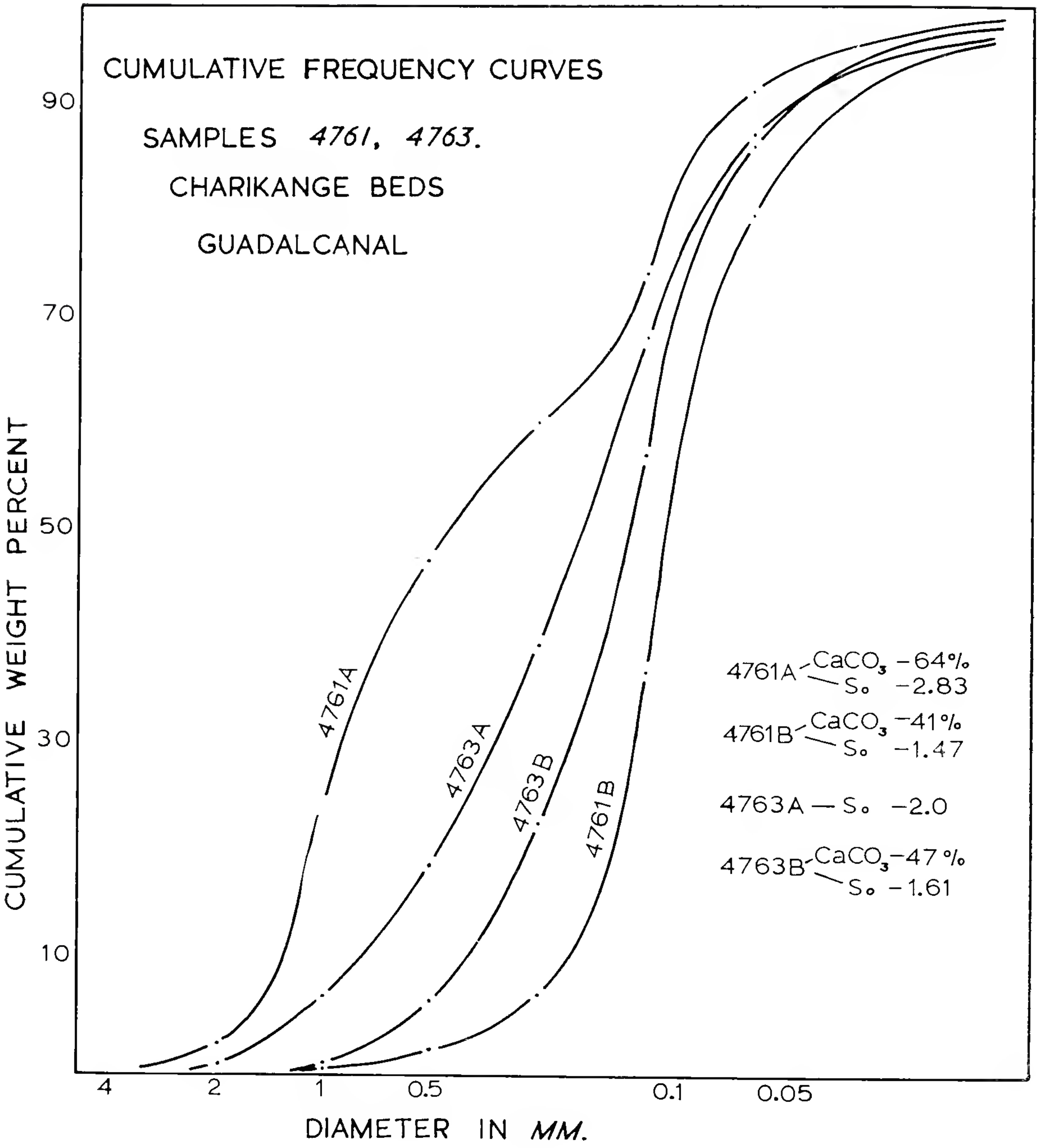


Fig. 3.

The larger foraminifera include both original specimens and those derived from the underlying Tina Calcarenite and the Betilonga Limestone. The latter are easily distingushed. They always have at least a partial coating of crystalline limestone; they are worn, frequently broken, and have a distinctive crystalline infilling. The remaining specimens are considered to be indigenous to the sediment for the following reasons: they are often well preserved so that those with flanges or delicate surface ornament are entire, contrasting with the shattered shells of most of the small molluscan species; they show a spread in sizes; some are partially air-filled and where infilling is present it is a yellowish clay, the same as that found in many of the smaller specimens, including the planktonic ones; the adherent matrix is common to the sediment. Finally, these indigenous larger foraminifera belong to species of *Lepidocyclina* (including *"Multilepidina"*), *Miogypsina*, *Cycloclypeus* (including subgenus *Katacycloclypeus*), *Planorbulinella*, *Gypsina* and *Operculina*, respectively, and so comprise what might be termed a normal fauna. This fauna has not been found in exposures of older sediments on Guadalcanal, even in the underlying older part of the Tangaraisu Shale; in any event this contains the same fauna of planktonic foraminifera as that of the Charikange Beds.

The fauna of smaller benthonic foraminifera was studied to obtain additional evidence on the nature of the original sedimentary environments. Thirty-nine of the sixty-two species of smaller foraminifera have been found also in modern sediments. Thirty-three of these species are benthonic forms, which provide information on the depth and possibly the bottom temperature.

It must be realised, however, that this kind of evidence has inherent limitations. Firstly, there are huge gaps in our knowledge of the ecological and geographical ranges of the species mentioned due to the inadequacy of the sample coverage of the Indo-Pacific province. Secondly, the concepts of some of the species are by no means clear. Thirdly, in the records of Recent species in the Indo-Pacific no distinction has been made between the occurrences of living and dead specimens. Hence, contamination of live assemblages by displaced dead specimens, which results in mixed death assemblages, cannot easily be recognised. Finally, many of the bathyal records might report displaced occurrences which cannot be confirmed and so the shallower occurrences are considered more reliable indices of the living environment of a species.

The following extant benthonic foraminifera are found in the Charikange Beds:

*Amphicoryna scalaris* (Batsch) 1791.
*Amphistegina lessonii* d'Orbigny, 1826.
*Anomalinella rostrata* (Brady), 1881.
*Bathysiphon fusca* Cushman, 1927.
*Bolivina hantkeniana* Brady, 1881.
*Bolivina schwageriana* Brady, 1881.
*Bulimina inflata* Seguenza, 1862.
*Cassidulina subglobosa* Brady, 1884.
*Cassidulina pacifica* Cushman, 1925.
*Ceratobulimina pacifica* Cushman and Harris, 1927.
*Cibicides refulgens* de Montfort, 1808.
*Cymbaloporella tabellaeformis* (Brady), 1884.
*Dentalina communis* (d'Orbigny), 1826.
*Dentalina subemaciata* Parr, 1950.
*Elphidium craticulatum* (Fichtel and Moll), 1798.
*Eponides margaritiferus* (Brady), 1881.
*Eponides praecinctus* (Karrer), 1868.
*Eponides procerus* (Brady), 1881.
*Eponides subornatus* (Cushman), 1921.
*Gyroidinoides neosoldanii* (Brotzen), 1936 (= Gyroidina soldanii (d'Orbigny) as used by Brady in 1884).
*Hyalinea balthica* (Gmelin), 1791.
*Islandiella limbata* (Cushman and Hughes), 1925.
*Nodosaria lamulifera* Boomgaart, 1949.
*Nodosaria pauperata* (d'Orbigny), 1846.
*Nodosaria spirostriolata* Cushman, 1917.
*Nonion pompilioides* (Fichtel and Moll), 1798.
*Planulina wuellerstorfi* (Schwager), 1866.
*Rectobolivina bifrons striatula* (Cushman), 1917.
*Rectobolivina columellaris* (Brady), 1881.
*Robulus costatus* (Fichtel and Moll), 1798.
*Robulus orbicularis* (d'Orbigny), 1826.
*Stilostomella abyssorum* (Brady), 1881.
*Stilostomella consobrina* (d'Orbigny), 1846.
*Uvigerina* spp.

Although there are more planktonic than benthonic specimens of foraminifera in the Charikange fauna, the fauna is mixed and so the evidence given by ratios of plantonic: benthonic foraminifera cannot be used to suggest the depth of deposition of the Charikange Beds. Considered separately, the planktonic species indicate open-sea conditions and possibly deep water with surface temperatures of about 25°-30°C. It could have been that conditions were similar to those off Guadalcanal today.

The benthonic element comprises a mixed fauna, in which species indicative of shallow-water environments are present with species suggestive of deep-water conditions. *Amphistegina lessonii*, *Anomalinella rostrata*, *Elphidium craticulatum*, Lepidocyclinidae, and Miogypsinidae indicate a shallow, warm water population. Further, *E. craticulatum* and *A. rostrata* seem to be common in warm, tropical waters not deeper than 40 fathoms in the Indo-Pacific. Such an assemblage probably represents an environment of similar depth to Polski's (1959) Central Shelf fauna (150-285 feet), but the bottom temperature probably was 20°-25°C.

A deep-water environment is suggested by the species *Cassidulina pacifica*, *Planulina wuellerstorfi*, *Bulimina inflata*, *Gyroidinoides neosoldanii*, *Nonion pompiloides*, *Rectobolovina bifrons striatula*, *Nodosaria spirostriolata*, *Stilostomella abyssorum* and *S. consobrina*. There are only a few depth records available for the last four of these species, all of them for depths of the order of 500 to 700 fathoms. The other five species have been recorded from shallow waters of less than 100 fathoms, but by far the great majority of their records are for depths of 500 fathoms or more. By and large this assemblage of species suggests an original environment roughly corresponding to Polski's Middle Bathyal fauna (2,000-4,500 feet and bottom temperatures of 6°-10°C.). As well, the species *Höglundina elegans* occurs higher in the Charikange Beds and this species has been recorded many times from deep water only.

This faunal evidence at least indicates that the Charikange Beds were formed by mixing of sediments. Marine sediments deposited in a shallow-water tropical environment, along with sediments from intermediate depths, were displaced to a depth of about 500 fathoms by slumping prior to consolidation of any of the sediments. Transportation by turbidity currents would thoroughly mix the sediments from the shallower depths, and these in turn would mix with the deep-water sediments accumulating at their ultimate position of rest.

### Conclusions on the Charikange Beds

The combination of evidence afforded by the regional field study and the sedimentary and faunal character of the samples examined, leads us to the following conclusions:

(1) The Charikange Beds were deposited rapidly in a tectonically unstable environment; the bulk of them are first-cycle sediments.

(2) Slumping or other transport played a part in the accumulation of the Charikange Beds.

(3) The association of larger and planktonic foraminifera was not due to the derivation of the former type from older consolidated sediments; it is best explained by contemporaneous transport by slumping or turbidity flow, which

carried natural life-assemblages of warm fairly shallow water benthonic foraminifera and their containing sediments into deeper water. This transport took place long before there was any consolidation of the sediments.

(4) The association now to be described was essentially contemporaneous.

### The Association

The following species of planktonic and larger benthonic foraminifera are found in samples 4761, 4762 and 4763. Qualitative estimates of frequency are given for each species. For the larger forms, if more than 25 specimens could be picked from about 100 gms of sediment the species is said to be abundant (a): if 11-25 specimens, common (c): if 5-10 specimens, frequent (f): if less than 5 specimens, rare (r): and if only one specimen could be picked, very rare (v). For the planktonic forms the same frequency range is based on about 5 gms of sediment.

*Larger Foraminifera*

| | 4761 | 4762 | 4763 |
|---|---|---|---|
| *Operculina complanata japonica* | a | c | a |
| *Lepidocyclina ("Multilepidina") suvaensis* | | c | a |
| *Operculina venosa* | c | f | c |
| *Cycloclypeus (C.) indopacificus* | c | f | f |
| *Lepidocyclina (N.) japonica* | f | f | r |
| *Miogypsina polymorpha* | r | f | |
| *Planorbulinella cf. larvata* | r | r | r |
| *Cyc. (Katacycloclypeus) martini* | r | r | r |
| *Gypsina squamiformis* | | r | v |
| *Lepidocyclina (N.) martini* | r | | |
| *Planorbulinella sp.* | | | v |
| *Heterostegina sp.* | | | v |

*Planktonic Foraminifera*

| | 4761 | 4762 | 4763 |
|---|---|---|---|
| *Globigerinoides conglobatus* | v | | |
| *G.-oides obliquus* | | | r |
| *G.-oides quadrilobatus immaturus* | r | f | f |
| *G.-oides quadrilobatus sacculifer* | v | v | r |
| *G.-oides quadrilobatus trilobus* | r | | c |
| *Globoquadrina altispira altispira* | r | | c |
| *G.-ina dehiscens advena* | r | | v |
| *G.-ina dehiscens dehiscens* | r | r | f |
| *Globorotalia scitula* | | | v |
| *G. sp. cf. G. tumida* | f | f | a |
| *Orbulina universa* | v | v | r |
| *Pulleniatina obliquiloculata* | r | r | r |
| *Sphaeroidinellopsis kochi* | r | | r |
| *S. seminulina* | a | c | a |
| *S. subdehiscens* | f | r | c |

### Notes on the Species

#### *Larger Foraminifera*

*Lepidocyclina ("Multilepidina") suvaensis* (Whipple) 1934—Plate 1. Figs. 9-14.

This is the same species as that described by Whipple as *L. (Cyclolepidina) suvaensis* from Fiji. It is found in other parts of the Indo-Pacific region and is usually considered to be of Burdigalian age. A number of specimens are figured to show variation in the nature of the nucleoconch and the usual presence of rays which can often be seen in equatorial section; this is a feature distinguishing it from otherwise similar species, e.g. *L. ("M.") luxurians* (Tobler) or *L. ("M.") irregularis* (Hanzawa). It should be stressed that the nucleoconch with two large chambers (Fig. 9) is a rare variant. Only two of about 100 specimens are like this: the remainder have from 3 to 7 chambers (the actual number may depend on the precise location of the thin section with respect to the plane of equatorial chambers).

Following the work of Van der Vlerk (1961) the internal features of the type of *L. radiata* (Martin) are now known for the first time. Their resemblance to those of the Guadalcanal specimens is striking as may be seen by a comparison between Van der Vlerk's description and illustrations with those in Coleman 1963*a* (Plates 3 and 4: note especially Figure 5 on Plate 4), and also the illustrations in this paper. It may well be that the Guadalcanal specimens should be referred to *L. radiata*. This possibility is left standing until more is known of the variation in topotypic specimens of that species. Van de Vlerk considers that the type of *L. radiata* came from sediments younger in age than Burdigalian.

The above remarks contribute to the problem of the significance of multilocular embryonic chambers in *Lepidocyclina*, and as a corollary to this, the concept and validity of *Multilepidina* and *Pliolepidina*, respectively (for references, see Cole 1963*a* and 1963*b*). Discussion of this problem, however, lies outside the aim of this paper.

*Lepidocyclina (Nephrolepidina) japonica* Yabe. 1906 — Plate 1, Figs. 7, 8.

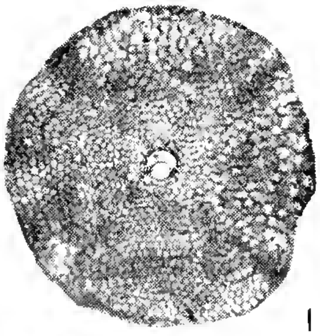
On Guadalcanal this species is also found in the Tina Calcarenite and the upper part of the Betilonga Limestone, but not in the lower part (of Aquitanian age) as stated previously by Coleman (1963*a*). Specimens which are clearly derived from these sediments are found in the Charikange Beds together with those considered to be indigenous.

*Lepidocyclina (N.) martini* (Schlumberger), 1900 — Plate 1, Fig. 1.

The lenticular shape without a marked central boss and the marked elongation of the equatorial chambers along the rays distinguish this species from the otherwise similar *L. (N.) radiata* (Martin) as it is generally conceived. According to Eames *et al.* (1962) *L. (N.) martini* is a Vindobonian species but it has been found as part of

### PLATE 1

1 : *Lepidocyclina (Nephrolepidina) martini* (Schlumberger) Equatorial section of UWA 50411. X20; 2 : *Planorbulinella* sp. cf. *P. larvata* (Parker and Jones) Transverse section of UWA 50412, X32; 3 : ? *Planorbulinella* sp. Median section of UWA 50413. X20; 4, 5 : *Miogypsina polymorpha* (Rutten) 4, transverse section of UWA 50414, X25; 5, part-median section of UWA 50415, X20; 6 : *Heterstegina* sp. cf. *H. suborbicularis d'Orbigny* Partial median section of UWA 50416, X30; 7, 8 : *Lepidocyclina (Nephrolepidina) japonica* Yabe 7, vertical section of UWA 50417, X13; 8, equatorial section of UWA 50418. X13; 9-14 : *Lepidocyclina ("Multilepidina") suvaensis* (Whipple) 9, central portion of equatorial section, UWA 50419, X25; 10, vertical section of UWA 50420, X11; 11, central portion of equatorial section, immature specimen, UWA 50421, X19; 12, equatorial section (slightly oblique) of UWA 50422, X19, showing elongation of hexagonal chamberlets along rays; 13, 14, external appearance of UWA 50423, X5, and UWA 50424, X5; 15 : *Cycloclypeus (Cycloclypeus) indopacificus* Tan Median section of UWA 50425, X13; 16-17 : *Cycloclypeus (Katacycloclypeus) martini* Van der Vlerk 16, median section of UWA 50426, X12; 17, external appearance of broken specimen, UWA 50427, X4.5; 18-20 : *Operculina complanata (Defrance) japonica* Hanzawa 18, external appearance of UWA 50428, X5; 19, median section of UWA 50429, X12; 20, median section of UWA 50430, X12, a more tightly coiled specimen.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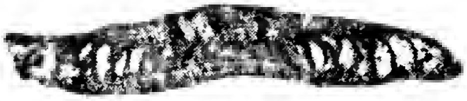
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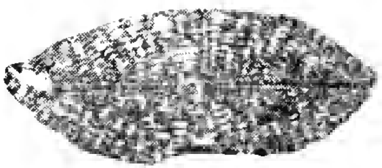
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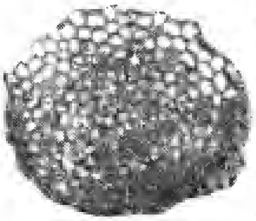
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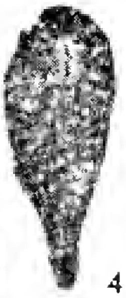
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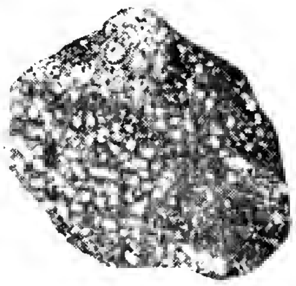
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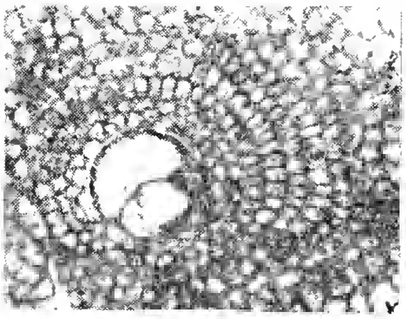
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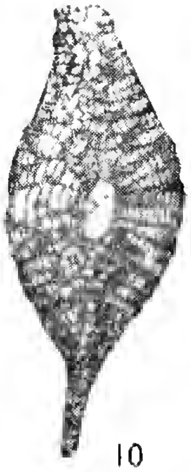
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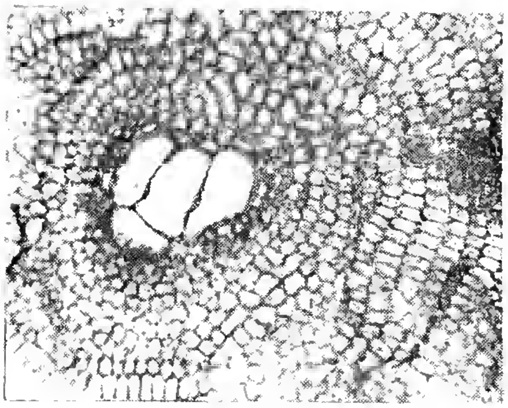
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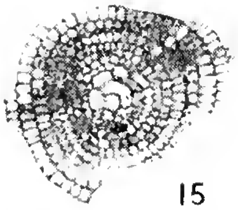
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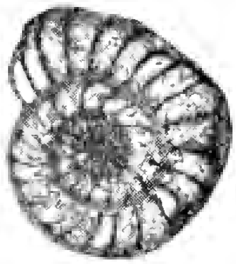
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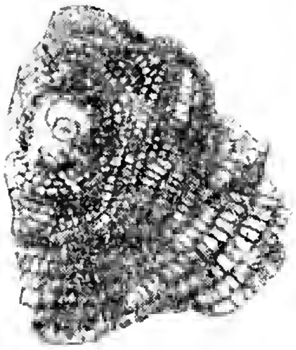
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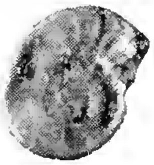
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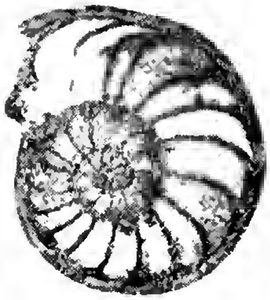
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Plate 1

typically Burdigalian assemblages (Coleman 1963*a*) in the Tina Calcarenite, the Bonege Limestone, the Lake Lee Calcarenite (Guadalcanal) and the Anuha Calcarenite (Florida).

*Miogypsina polymorpha* (Rutten), 1911 — Plate 1, Figs. 4, 5.

Specimens of this species derived from the upper part of the Betilonga Limestone are also found together with indigenous specimens. They cannot be distinguished morphologically.

*Cycloclypeus (Cycloclypeus) indopacificus* Tan, 1932 — Plate 1, Fig. 15.

This species is common in the Indo-Pacific region in sediments of Vindobonian age, but it occurs also in Burdigalian sediments on Guadalcanal (Bonege Limestone, Lake Lee Calcarenite) on Florida (Anuha Calcarenite) and also on Fiji (in the "*Lepidocyclina* Tuff", see Eames *et al.* 1957).

*C. (Katacycloclypeus) martini* Van der Vlerk, 1923 — Plate 1, Figs. 16, 17.

Species of this subgenus are characteristic of the Burdigalian. It has not been recognised with certainty from other Solomon Islands sediments.

*Operculina complanata japonica* Hanzawa, 1935 — Plate 1, Figs. 18-20.

Specimens of this subspecies show great variation, the extremes of which are connected by a continuous series of intergrading specimens. It is present in flood proportions in the Charikange Beds but is rare in other Solomon Islands sediments of about the same age.

*O. venosa* (Fichtel and Moll), 1798.

Probably the most common species found in Solomon Islands Tertiary and Quaternary sediments, *O. venosa* is also present in great numbers in the present-day beach sands. The oldest specimens do not appear to be in any way different from the modern ones.

*Planorbulinella* sp. cf. *larvata* (Parker and Jones), 1865 — Plate 1, Fig. 2.

Although referred to *P. larvata* this is almost certainly a new species having as its major distinguishing feature a laminated central portion; the laminations are the result of lateral extensions of the chamber walls (see Coleman, 1963*a*) and do not appear to represent a gerontic feature. It is especially characteristic of Burdigalian to Quaternary sediments in the Solomon Islands.

*Planorbulinella* sp. — Plate 1, Fig. 3.

This rare species has been seen in thin sections of the Charikange samples.

*Gypsina squamiformis* Chapman, 1900.

The Moluccan form described under this name by Bursch (1947) also occurs in the Charikange samples.

*Heterostegina* sp. — Plate 1, Fig. 6.

Only two specimens of this species have been seen, both in thin section. Its features are not sufficiently clear to permit a specific identification but it could well be *H. suborbicularis* d'Orbigny, a Pacific region Quaternary species. Cole (1957) records it from Eocene sediments from Eniwetok Atoll.

### *Plantonic Foraminifera*

*Globigerinoides conglobatus* (Brady), 1879 — Plate 2, Figs. 15, 16, 21.

One poorly preserved specimen seems to belong here. Banner and Blow (1960) gave the range of *G. conglobatus* as Pliocene to Recent, and they pointed out that certain Eocene and Lower Miocene records attributed to *G. conglobatus* are of other species. Belford (1962) recorded this species from the Upper Miocene of Papua-New Guinea, and Umbgrove (1931, p. 63) listed it from Miocene 'f' to Recent of Indonesia.

This species is most abundant in the equatorial part of the Pacific, in waters ranging from 16°C. to 33°C. (Bradshaw 1959). In the Indian Ocean it is present in the central and equatorial water masses (Beliaeva 1962), where the surface water temperatures range from 10°C. to 28°C.

*Globigerinoides obliquus* Bolli, 1957 — Plate 2, Figs. 10, 17.

This species is rare in the Charikange Beds. The absolute range recorded for this species in the Caribbean region is from the *Globorotalia kugleri* zone (Upper Oligocene) to the *Globigerina bulloides* zone of Upper Miocene age (Bolli 1957; Blow 1959). Belford (1962) has rare specimens from the Middle Miocene of Papua. Its range in the Solomon Islands is from Upper Oligocene to Upper Miocene-Pliocene.

*Globigerinoides quadrilobatus immaturus* (LeRoy), 1939 — Plate 2, Figs. 11, 18.

This subspecies can be distinguished from *G. quadrilobatus trilobus* (Reuss) by its more highly arched umbilical aperture and the less embracing ultimate chamber although transitional forms are difficult to place with certainty. In

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**PLATE 2**

1 : *Sphaeroidinellopsis subdehiscens* (Blow) Umbilical view, UWA 49146, X75; 2-4 : ? *Pulleniatina obliquiloculata* (Parker and Jones) 2, lateral view; 3, umbilical view; 4, dorsal view; UWA 49149, X75; 5, 8 : *Sphaeroidinellopsis seminulina* (Schwager) 5, umbilical view of *multiloba*-type, UWA 49159, X60; 8, umbilical view of typical form, UWA 49147, X60; 6, 13, 14 : *Globoquadrina dehiscens advena* Bermudez 6, lateral view; 13, dorsal view; 14, umbilical view; UWA 49143, X60; 7, 9 : *Globigerinoides quadrilobatus trilobus* (Reuss) 7, dorsal view; 9, umbilical view; UWA 49139, X75; 10, 17 : *Globigerinoides obliquus* Bolli 10, umbilical view; 17, dorsal view; UWA 49141, X100; 11-18 : *Globigerinoides quadrilobatus immaturus* (LeRoy) 11, umbilical view; 18, dorsal view; UWA 49137, X75; 12, 19 : *Globoquadrina dehiscens dehiscens* (Chapman, Parr and Collins) 12, umbilical view; 19, dorsal view; UWA 49144, X60; 15, 16, 21 : *Globigerinoides conglobatus* (Brady) 15, umbilical view; 16, dorsal view; 21, lateral view, UWA 49140, X60; 20, 23, 24 : *Globoquadrina altispira altispira* (Cushman and Jarvis) 20, umbilical view; 23, lateral view; 24, dorsal view; UWA 49142, X75; 22 : *Orbulina universa* d'Orbigny UWA 49145, X50; 25, 26, 30 : *Sphaeroidinellopsis kochi* (Caudri) 25, dorsal view; 26, umbilical view; 30, lateral view; UWA 49148, X60; 27, 31-33, 37, 38 : *Globorotalia* cf. *G. tumida* (Brady) 27, lateral view; 31, umbilical view; 32, dorsal view; UWA 49136b, X75. 33, lateral view; 37, dorsal view; 38, umbilical view; UWA 49136a, X100; 28, 28 : *Globigerinoides quadrilobatus sacculifer* (Brady) 28, umbilical view; 29, dorsal view; UWA 49138, X75; 34-36 : *Globorotalia scitula* (Brady) 34, umbilical view; 35, dorsal view; 36, lateral view; UWA 49094, X60.

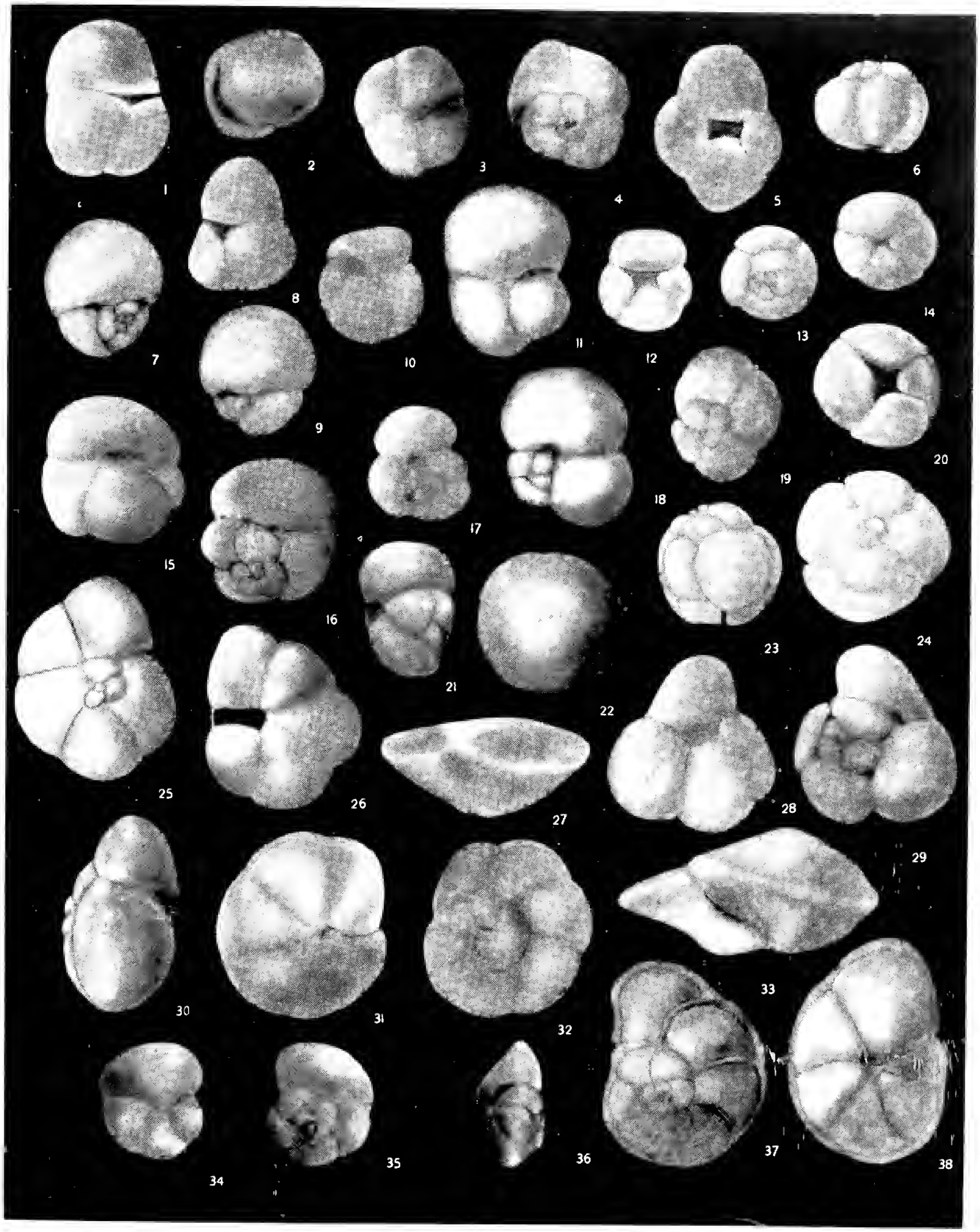
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Plate 2

the Solomons this subspecies ranges from the Aquitanian to the Upper Miocene-Pliocene, but previous records from the Indo-Pacific region extend its range into the Upper Oligocene.

*Globigerinoides quadrilobatus sacculifer* (Brady), 1877 — Plate 2, Figs. 28, 29.

The specimens from the Charikange fauna are most like the lectotype of *G. quadrilobatus sacculifer* chosen by Banner and Blow (1960). Although a transitional series between *G. quadrilobatus irregularis* LeRoy and this subspecies could be recognised in the Charikange fauna, no attempt was made to separate these subspecies in this work.

This cosmopolitan species is well represented in Noegene to Recent sediments of the Indo-Pacific region (Umbgrove 1931: LeRoy 1941; Crespin 1963; Chang 1959: Belford 1962). Bradshaw (1959) found it in Pacific waters ranging in surface temperature from 15°C. to 33°C., but it was most common between 25°C. and 29°C. In the Indian Ocean it is present in the tropical and central parts with a temperature range of 10°C.—28°C., according to Beliaeva (1962).

*Globigerinoides quadrilobatus trilobus* (Reuss), 1850 — Plate 2, Figs. 7, 9.

This subspecies of *G. quadrilobatus* has been separated from *G. quadrilobatus immaturus* by characters of its final chamber, which is more inflated and more embracing, and by the more elongate, narrower primary aperture. A cosmopolitan subspecies, *G. quadrilobatus trilobus* first appeared in the Lower Miocene and has persisted to the present. It has been widely recorded from the Indo-Pacific region.

*Globoquadrina altispira altispira* (Cushman and Jarvis), 1936 — Plate 2, Figs. 20, 23, 24.

Although the poor preservation of specimens assigned to *Globoquadrina* has destroyed or obscured details of the umbilical teeth which especially distinguish this genus, the specimens possess other features of the test which characterise known specimens of *Globoquadrina*, in particular *G. altispira altispira*.

This species is distinguished from *G. dehiscens dehiscens* by its high trochoid spire and the axially elongate chambers; an otherwise similar subspecies, *G. altispira globosa*, has globular and less elongate chambers in the last whorl. Although previous records indicate that *G. altispira altispira* became extinct late in the Burdigalian or early in the Helvetian, Chang's (1959) Upper Miocene record from Taiwan and Belford's (1962) observation of the species in strata dated as Pliocene from Papua-New Guinea, might be taken as evidence for a markedly longer range for *G. altispira altispira* in the equatorial part of the Indo-Pacific than elsewhere. However, Chang's [illegible] is doubtful, because two of his figured specimens (Chang 1959, Plate 2, Figs. 8a-9c) belong to other forms of *Globoquadrina*. Belford's identifications, on the other hand, seem correct but the age determinations of some of his younger faunas may be in error. Although this evidence is equivocal, additional records from Wreck Island (Lloyd 1961) and the Solomons (McTavish 1963) showed that *G. altispira altispira* probably became extinct late in the Tertiary 'f'. It seems likely that the range for this species is Aquitanian to Tortonian.

*Globoquadrina dehiscens advena* Bermudez, 1949 — Plate 2, Figs. 6, 13, 14.

The range for this subspecies seems to be closely similar to that of *G. altispira altispira* except that it probably became extinct earlier in the Tortonian, as it does in the Solomons.

*Globoquadrina dehiscens dehiscens* (Chapman, Parr and Collins), 1934 — Plate 2, Figs. 12, 19.

The Charikange specimens generally agree with those figured by Blow (1959) and Jenkins (1960), in which the apertual face is neither as prominent nor as smooth as that of the holotype. The first chamber of one specimen seems to be divided into two, thus giving the appearance of five chambers in the last whorl.

This species is moderately long-ranging with a wide distribution. It ranges from Middle or Upper Oligocene to Upper Miocene, but it is most common in the Lower and Middle Miocene. In the Solomons *G. dehiscens* became extinct in the *Sphaeroidinellopsis seminulina* fauna or Tertiary Upper 'f' age.

*Globorotalia scitula* (Brady), 1882 — Plate 2, Figs. 34-36.

A single, typical specimen of *G. scitula* has been found in the Charikange fauna. Although the range of *G. scitula (sensu lato)* is Aquitanian to Recent according to Blow (1959), the species is only present in Vindobonian and younger sediments of the British Solomon Islands. It has been found in small numbers over a wide range of temperatures (12°C.—29°C.) in the Pacific (Bradshaw 1959).

*Globorotalia* sp. cf. *G. tumida* (Brady), 1877 — Plate 2, Figs. 27, 31-33, 37, 38.

This is an extremely variable species, and its variation is much greater than that found in Upper Miocene populations of *G. tumida* from Guadalcanal. The more obvious variation is in the shape of the chambers and the outline of the periphery. However, there is variation in the numbers of chambers in the last whorl, commonly five to seven with eight in rare specimens. Further, there is a range in the convexity of the spiral, but spiro-convex specimens appear to be rare.

Some specimens with only a slightly convex spiral side are strongly reminiscent of *G. cultrata fijiensis* Cushman, *G. fohsi robusta* Bolli, and *G. cultrata multi-camerata* Cushman and Jarvis. In this respect, it is interesting to note that Banner and Blow (1960, p. 27) have suggested that *G. fohsi robusta* is pseudomorphous after *G. tumida*. Still other specimens which appear to be spire-convex are not unlike *G. cultrata panda* Jenkins. However, all these specimens can be related to *G.* cf. *G. tumida* because of their tumid tests and because there are specimens gradational between them and forms more like typical *G. tumida*. There are other specimens that should perhaps be referred to *G. cultrata menardii*. They have raised sutures and are less tumid than most other specimens from the Charikange Beds. However, they are connected to specimens like typical *G. tumida* by transitional forms, so they have been included in *G.* cf. *G. tumida* too.

Banner and Blow (1960, p. 27) suggested that typical *G. tumida* did not become distinct from *G. cultrata menardii* until Upper Miocene time although representatives of it first appeared in the Upper Tortonian. Evidence from Guadalcanal supports this belief (McTavish 1963). Indeed, *G.* cf. *G. tumida* might be nothing more than a primitive population of *G. tumida*.

*Globorotalia tumida* is a tropical species. In the Pacific it is most common between temperatures of 29°C. and 31°C. and is not present in water at surface temperatures less than 19°C. (Bradshaw 1959). Beliaeva (1962, p. 10) recorded it from the Arabian and equatorial waters of the Indian Ocean where the surface-water temperature ranged from 23°C. to 28°C.

*Orbulina universa* d'Orbigny, 1839 — Plate 2, Fig. 22.

The specimens of *O. universa* are poorly preserved. The ultimate chamber of these specimens appears to embrace the preceding chambers completely and the test bears pore-like apertures and finer pores over its surface.

Since LeRoy's first important paper (LeRoy 1948) on the *Orbulina*-surface a large literature on the occurrence of this species has grown, and it seems widely accepted that pre-Miocene records of *O. universa* are based on misidentifications or incorrect stratigraphical information. Recent evidence (Carter 1958; Cita and Elter 1960; and Glaessner 1959, 1960) from widely separated areas of the Indo-Pacific region and Europe indicates that *Orbulina* definitely made its entry in post-Aquitanian times and suggests that it first appeared early in the Helvetian.

*Pulleniatina obliquiloculata* (Parker and Jones), 1862 — Plate 2, Figs. 2-4.

Specimens earlier referred doubtfully to *Globorotalia opima continuosa* Blow (McTavish 1963, p. 294) now seem more likely to be primitive forms of *P. obliquiloculata* rather reminiscent of *Globigerina nipponica* Asano. Possibly this latter species is the juvenile stage of *P. obliquiloculata* for it is markedly smaller than adult specimens of this species and is not unlike the assumed primitive forms of *P. obliquiloculata* found in the Charikange Beds. Banner and Blow (1960) believed that typical *P. obliquiloculata* ranged from the Pliocene to the Recent. However, it appears to range from late in the Tortonian (= Tertiary Upper 'f') to the Recent in the Indo-Pacific region where it has been widely recorded. Its range in the Solomons is consistent with the latter view.

*Sphaeroidinellopsis kochi* (Caudri), 1934 — Plate 2, Figs. 25, 26, 30.

This species is rare in the Charikange fauna. It differs from *S. seminulina* in having five or six, occasionally seven, chambers in the last whorl, a more open umbilicus, arched aperture, and radially elongate chambers. Glaessner (1943, p. 69) listed *S. kochi* as a Miocene guide-fossil in the Indo-Pacific. Evidence from Venezuela (Blow 1959) and the Solomons (McTavish 1963) suggests that this species existed only during the Middle Miocene.

*Sphaeroidinellopsis seminulina* (Schwager), 1866 — Plate 2, Figs. 5, 8.

*Sphaeroidinellopsis seminulina* is the most common planktonic species in the Charikange fauna. Specimens of *S. multiloba* (LeRoy) have been included in *S. seminulina* in the belief that they represent a mature stage of this species. Accordingly, *S. seminulina* has been recognised by the three or four chambers in the last whorl with the last chamber being considerably smaller than the combined size of those preceding it. Glaessner (1943, p. 69) listed this species as a Miocene guide-fossil for the Indo-Pacific region, where it has been recorded from such widely separated areas as Borneo, Taiwan, New Zealand and Australia. In the Solomons it is present in sediments ranging in age from Burdigalian to Tortonian. Rare specimens in Upper Miocene sediments are probably reworked.

*Sphaeroidinellopsis subdehiscens* (Blow), 1959 — Plate 2, Fig. 1.

Banner and Blow (1960) chose *S. subdehiscens* as the type species of their new genus *Sphaeroidinellopsis*, which is distinguished from *Sphaeroidinella* by its lack of supplementary apertures. The last chamber of *S. subdehiscens* is more or less equal to the preceding two chambers and this is the features which best distinguishes it from *S. seminulina*. However, transitional forms between these species are present in the Charikange Beds. *S. subdehiscens* is confined to the Middle Miocene and the early Upper Miocene. In the Indo-Pacific region it has been found in Taiwan, Sylvania Guyot and Papua-New Guinea. In the Solomons it is present in the Middle Miocene *Globigerina nepenthes* and *Sphaeroidinellopsis seminulina* faunas and small numbers have been recognised in the basal part of the Upper Miocene *Globigerina dutertrei* fauna.

### Age Significance

If considered alone, the larger foraminifera from the Charikange Beds samples would be thought to comprise a Burdigalian or an early Vindobonian assemblage. The following species are regarded as essentially Burdigalian (Tertiary $f_{1-2}$): *Lepidocycline* (*"Multilepidina"*) *suvaensis*, *Miogypsina polymorpha*, *Cycloclypeus* (*Katacycloclypeus*) *martini*, *Lepidocyclina* (*Nephrolepidina*) *japonica*. A Vindobonian age is suggested by the presence of *L.* (*N.*) *martini* and *C.* (*C.*) *indopacificus;* both these species may be found in older sediments of Burdigalian age. The suggestion of a late Burdigalian to early Vindobonian age is a compromise and not a studied calculation; it probably exceeds the limits of refinement possible with larger foraminifera during this part of the Tertiary. So far as the planktonic foraminifera are concerned the abundance of species of *Sphaeroidinellopsis*, especially *S. seminulina*, with species of *Globoquadrina*, indicate that this association should be correlated with the *Sphaeroidinellopsis seminulina* fauna as it is expressed in the Malaita Group in the Solomon Islands. This Malaitan fauna was correlated in turn (McTavish 1963, pp. 68-69) with the *Sphaeroidinella seminulina* zone of Venezuela (see Blow 1959) which is shown by Blow and Banner (1962, p. 137) as spanning the Tortonian-Sarmatian boundary.

The older age limit of this zone has not yet been established and so it would be too specific at this stage to restrict the Malaitan *Sphaeroidinellopsis seminulina* fauna to the Tortonian, a younger age than is indicated by the larger foraminifera, although the stratigraphic position of the Charikange samples would support this assignation. We have been content therefore to describe this association as simply Vindobonian. Nevertheless, if it is indeed true that the foraminifera preserved in the samples were contemporaneous, then the possibility remains that the following species of larger foraminifera survived into Tortonian time: *Lepidocyclina ("Multilepidina") suvaensis* (Whipple), *Lepidocyclina (Nephrolepidina) japonica* Yabe, *Miogypsina polymorpha* (Rutten), *Cycloclypeus (Katacycloclypeus) martini* Van der Vlerk, and *Operculina complanata japonica* Hanzawa.

### Acknowledgments

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# 5.—Discontinuous and Presumed Vicarious Plant Species in Southern Australia

By J. W. Green*

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The details of distribution of discontinuous and presumed vicarious species pairs in south-western and south-eastern Australia are presented. Selected discontinuous species are listed and their distributions shown on outline maps, and these species are discussed in relation to the geological and climatic history of the Australian continent. It is suggested that some disjunctions may have their explanation in long-distance wind dispersal. Presumed vicarious species known to occur in the two regions are listed, and are discussed in relation to discontinuous species and geological and climatic history.

## Introduction

Comparison of the vascular floras of south-western and south-eastern Australia has revealed the existence of several hundred species in common, of which some 35 have been selected for study according to the principles outlined in the section below entitled "Discontinuities between South-western and South-eastern Australia".

All are autochthonous species whose disjunction is well marked and which have no obvious mechanism whereby they may be dispersed over long distances by water or by animals. All but a few are restricted to the temperate area of southern Australia shown in Figure 1.

In addition, about 50 pairs of presumed vicarious species have so far been noted in the two regions.

The only previous comparison of the vascular plants of the two regions at the specific level appears to be that of Hooker (1860), who stated that 83 species were common to south-western and south-eastern Australia. He gave the number of such species for each genus but mentioned no specific names.

## Discontinuous Species

The area occupied by a species is usually said to be discontinuous (or disjunct) if it is broken into two or more portions which are separated by a distance exceeding the "normal dispersal capacity" (Cain 1944) of propagules of the species. The determination of dispersal capacity must depend on experimental data, but an estimate of dispersal capacity may be obtained from the size and morphology of the propagules. Discontinuity may be assumed if the actual distance separating the populations exceeds this estimate.

### *Minor Discontinuities in Eastern Australia*

In central and south-eastern Australia several examples of discontinuities are well known. *Eucalyptus cladocalyx* is of particular interest because of its discontinuous occurrences on Eyre Peninsula, Kangaroo Island and in the Flinders Range, even though the tree has been planted successfully in intervening areas, proving the suitability, at least for growth, of such habitats.

Other examples are *Acacia peuce*, occurring in several separated localities in central Australia and south-western Queensland, *Eucalyptus globulus* and *E. regnans*, both occurring in south-eastern Australia and Tasmania, *Dillwynia oreodoxa*, restricted to the Victorian Grampians and the Braidwood-Clyde Mountains area of New South Wales, *Schoenus turbinatus*, *Lasiopetalum ferrugineum* and *Phebalium dentatum*, all of which are discontinuous between the Sydney district and the Gibraltar Range in northern New South Wales, and *Eucalyptus nitens*, which is discontinuous between the northern and southern tablelands of New South Wales.

Specht *et al.* (1961) have described the disjunct distribution of *Eucalyptus elaeophora* (now to be known as *E. goniocalyx*, according to Johnson 1962) in South Australia, Victoria and New South Wales, while Willis (1962) mentions several examples of Tasmanian plants which are found only in the Grampians in mainland Australia (e.g. *Leptospermum nitidum* and *Pomaderris apetala*), a number of disjunctions between the Grampians and the area from East Gippsland to central coastal New South Wales (*Psilotum nudum*, *Davallia pyxidata*, *Howittia trilocularis*, *Dodonaea truncatiales*, and *Westringia glabra*) and one species which is unknown between the Grampians and north-eastern New South Wales (*Swainsona brachycarpa*).

The distances between the disjunct areas of the above species are mostly smaller than those of the species mentioned below, and some may well prove to be continuous when more information on dispersal capacity becomes available.

### *Discontinuities between South-western and South-eastern Australia*

The examples listed below were obtained by a study of the published literature, combined with the examination of specimens from several Australian herbaria. No critical taxonomic work has yet been done, but in most cases specimens from the south-western and south-eastern populations of each species have been compared in their gross morphology.

On the basis of distance, these may be classed as major discontinuities. Most are separated by about 750 miles, and a few by a greater distance. It is not considered likely that

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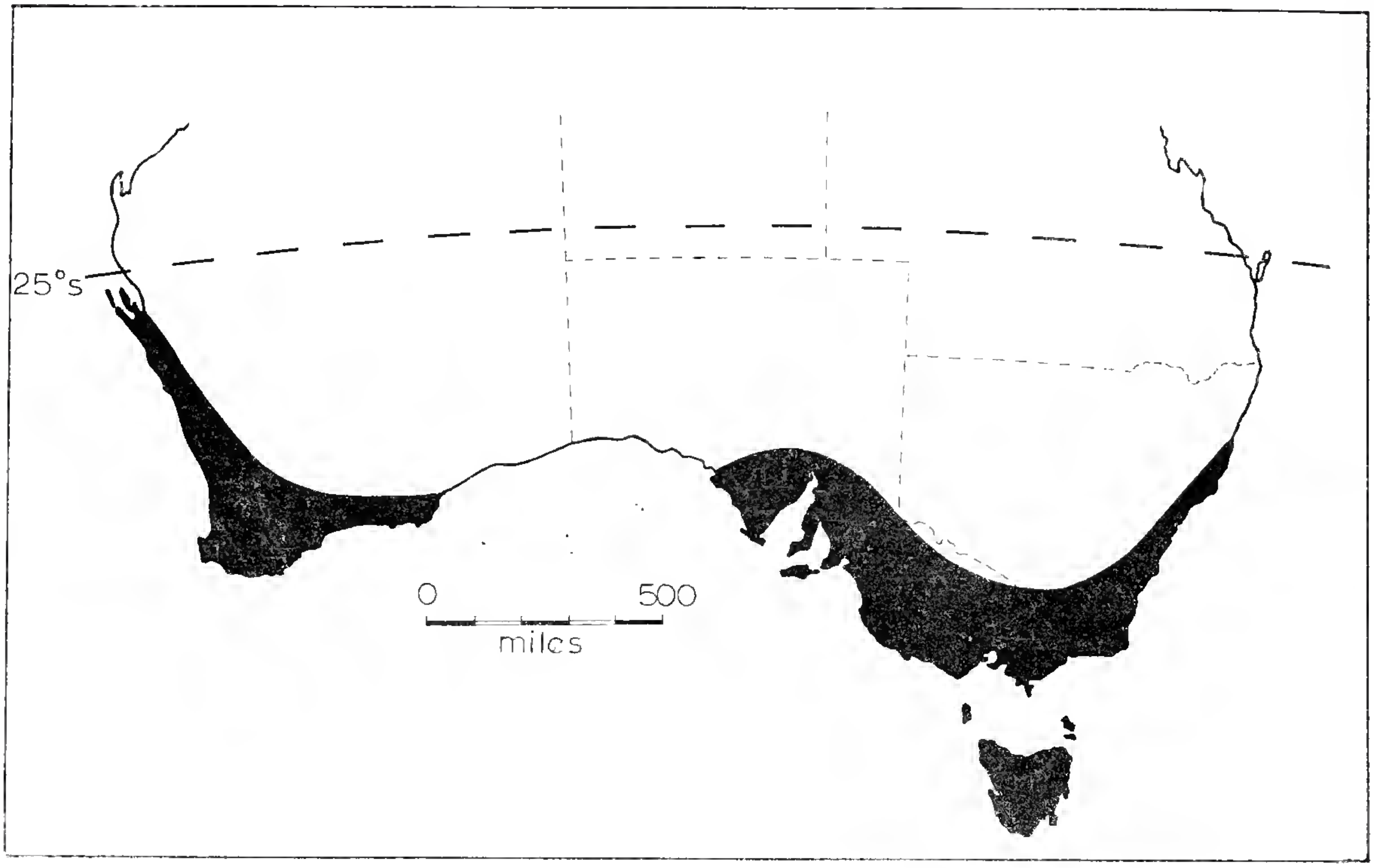


Fig. 1

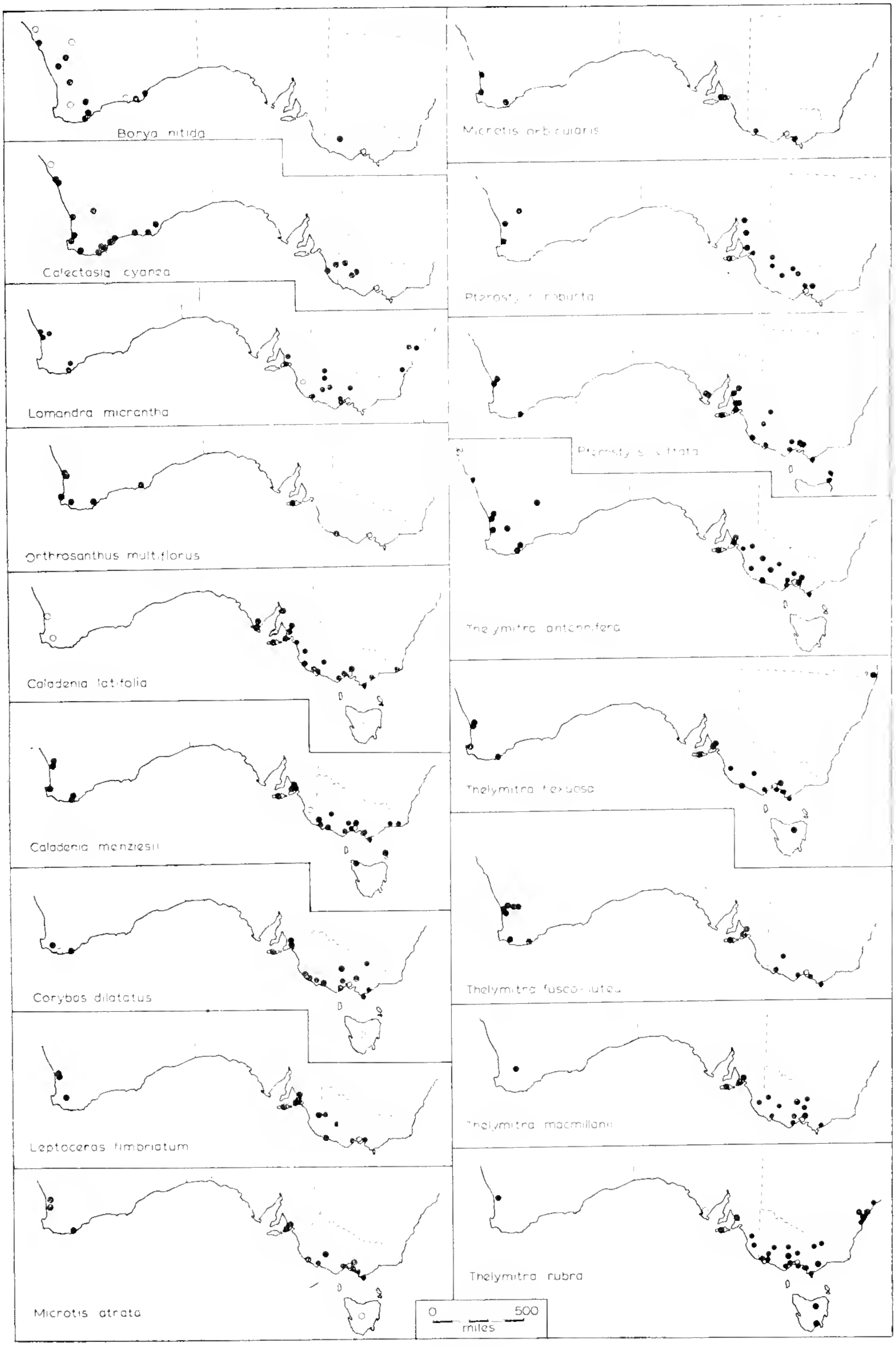
additional collections would extend the ranges much further into the intervening area; the Nullarbor Plain is noted for its paucity of species, and the sclerophyll communities in which the majority of the species occur are certainly absent. In any case the existing habitat conditions suggest that their survival would be impossible.

It is considered that the distances involved here are probably greater than the normal dispersal capacity of propagules of these species.

In selecting a short list for study, the following classes of plants were eliminated from the several hundred apparently discontinuous species mentioned in the Introduction: (i) species capable of growing in semi-arid regions, because of their potential capacity of migration between the two regions by marginal spread; (ii) littoral species, because they are presumably capable of marginal spread along the coast, or dispersal by sea water or animals of the shore, without any great problem in establishment; and (iii) aquatic species of rivers and lakes, again without any apparent problems in dispersal or establishment. For the sake of simplicity, species having any occurrence outside temperate Australia and Tasmania have also been eliminated. The remainder, then, are those species whose disjunctions are most difficult to explain.

The species are listed below and their ranges are shown on the maps in Figures 2-3.

- LILIACEAE
  - *Borya nitida* Labill.
  - *Calectasia cyanea* R.Br.
  - *Lomandra micrantha* (Endl.) Ewart
  - *Thysanotus tenellus* Endl.
  - *T.* sp. (undescribed)
- IRIDACEAE
  - *Orthrosanthus multiflorus* Sweet
- ORCHIDACEAE
  - *Caladenia latifolia* R.Br.
  - *C. menziesii* R.Br.
  - *Corybas dilatatus* Rupp et Nicholls
  - *Leptoceras fimbriatum* Lindl.
  - *Microtis atrata* Lindl.
  - *M. orbicularis* Rogers
  - *Pterostylis robusta* (Ewart) Rogers
  - *P. vittata* Lindl.
  - *Thelymitra antennifera* Hook.f.
  - *T. flexuosa* Endl.
  - *T. fusco-lutea* R.Br.
  - *T. macmillanii* F.Muell.
  - *T. rubra* Fitzg.
- PAPILIONACEAE
  - *Daviesia brevifolia* Lindl.
  - *Dillwynia cinerascens* R.Br.
  - *D. uncinata* (Turcz.) J.M.Black
  - *Sphaerolobium daviesiodes* Turcz.
  - *S. vimineum* Sm.
- RUTACEAE
  - *Microcybe pauciflora* Turcz.
- POLYGALACEAE
  - *Comesperma polygaloides* F.Muell.
- RHAMNACEAE
  - *Cryptandra leucophracta* Schlecht.
- STERCULIACEAE
  - *Thomasia petalocalyx* F.Muell.
- EPACRIDACEAE
  - *Acrotriche cordata* (Labill.) R.Br.
  - *Leucopogon hirsutus* Sond.
- LOGANIACEAE
  - *Logania vaginalis* (Labill.) F.Muell.
- STYLIDIACEAE
  - *Levenhookia pusilla* R.Br.
  - *Stylidium perpusillum* Hook.f.
- COMPOSITAE
  - *Lagenophora huegelii* Benth.


Borya nitida
Calectasia cyanea
Lomandra micrantha
Orthrosanthus multiflorus
Caladenia latifolia
Caladenia menziesii
Corybas dilatatus
Leptoceras fimbriatum
Microtis atrata
Microtis orbicularis
Pterostylis robusta
Pterostylis vittata
Thelymitra antennifera
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Thelymitra fusco-lutea
Thelymitra macmillanii
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Fig. 2

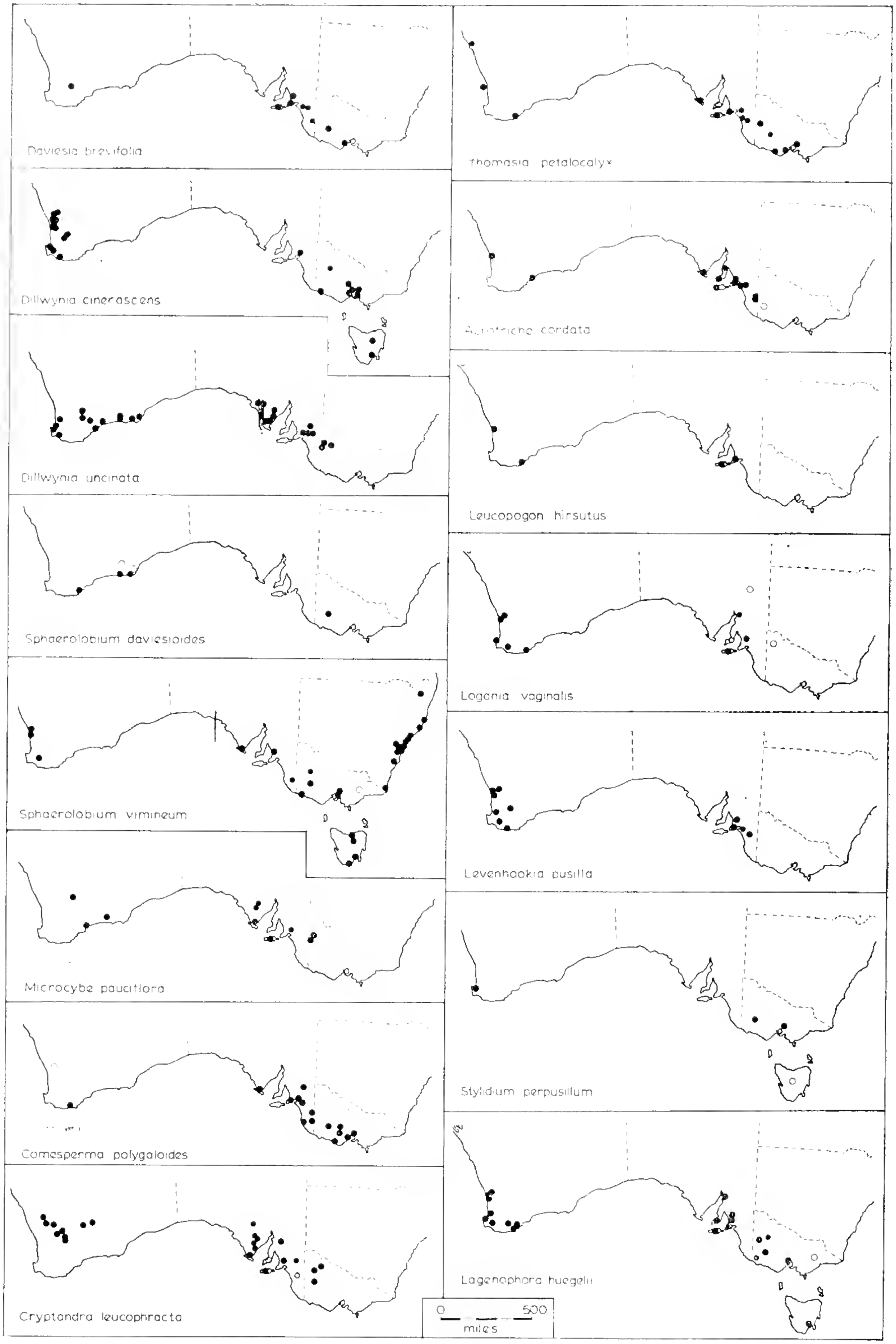
Daviesia brevifolia
Dillwynia cinerascens
Dillwynia uncinata
Sphaerolobium daviesioides
Sphaerolobium vimineum
Microcybe pauciflora
Comesperma polygaloides
Cryptandra leucophracta
Thomasia petalocalyx
Acrotriche cordata
Leucopogon hirsutus
Logania vaginalis
Levenhookia pusilla
Stylidium perpusillum
Lagenophora huegelii
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Fig. 3

There is no marked tendency for the majority of the species studied to be more widely distributed in either south-western or south-eastern Australia. *Borya nitida*, *Calectasia cyanea* and *Orthrosanthus multiflorus* are principally western with a limited occurrence in the east, while the reverse is true of *Sphaerolobium vimineum*, *Comesperma polygaloides*, and many of the orchids. *Leucopogon hirsutus* is very restricted in both regions. Three species, *Lomandra micrantha*, *Dillwynia cinerascens* and *Sphaerolobium daviesioides* have noticeably different forms in the two areas, the second being discussed in more detail below. *Thelymitara flexuosa* occurs in three separated areas, the eastern disjunction being over 750 miles. The widest disjunction is that of *Stylidium perpusillum*, which is not recorded between Busselton, Western Australia, and western Victoria, a distance of 1,560 miles.

It has been possible to pay special attention to the two species of *Dillwynia* which are discontinuous between the south-western and south-eastern regions. A large range of specimens has been examined from both regions showing that *D. uncinata* is markedly uniform in gross morphology over its entire area, while the disjunct populations of *D. cinerascens* seem to be morphologically distinct. All western specimens of the latter have spinescent branch-endings while all eastern specimens have none, and it appears that the two populations represent a pair of vicarious subspecies.

### Presumed Vicarious Species

Closely allied to the concept of discontinuous species distributions is that of vicarious pairs or sets. The history of the latter has been summarized by Cain (1944) who defines vicarious species as "closely related allopatric species which have descended from a common ancestral population and attained at least spatial isolation." They are thus the equivalent of the *Artenkreise* of Rensch. As pointed out by Vierhapper (1919) (quoted by Löve 1954), it is possible to visualise two ways in which corresponding taxa in different areas may have arisen: (i) as *true vicariads*, which have penetrated into a new area and later become differentiated, and (ii) as *false vicariads* or *substitution taxa*, which have differentiated prior to their occupation of new areas. Löve is of the opinion that the terms *vicariism*, *vicariad* and *vicarious* should be confined to the second type, and suggests that where lack of information permits no such subdivision, only the collective term *corresponding taxa* should be used. This would apply to the Australian examples quoted below.

The concept of vicariism has been applied to taxonomic ranks other than species but, as mentioned by Turrill (1959), the phytogeographical significance of vicarious families, tribes or genera is often obscure. The concept has also been applied to communities.

The accompanying list (Table I) shows pairs of species in which the members of each pair appear to be closely related systematically and far removed geographically. In most cases Bentham's *Flora Australiensis* has been the primary source of information, and it has been verified that Bentham considered the species of each pair closely related. In some cases (marked with an asterisk) Bentham actually commented on the closeness of the relationship. Wherever appropriate more recent monographs and revisions have been consulted.

| South-western species | South-eastern species |
|---|---|
| CYPERACEAE | |
| *Lepidosperma angustatum* R.Br. | *L. concavum* R.Br. |
| *L. gracile* R.Br. | *L. semiteres* F. Muell. ex Boeck. |
| *L. leptophyllum* Benth. | *L. tortuosum* F. Muell. |
| LILIACEAE | |
| *Lomandra caespitosa* (Benth.) Ewart | *L. sororia* (F. Muell. ex Benth.) Ewart |
| *Xanthorrhoea preissii* Endl. | *X. quadrangulata* F. Muell. |
| CASUARINACEAE | |
| **Casuarina decussata* Benth. | *C. torulosa* |
| *C. trichodon* Miq. | *C. stricta* Ait. |
| PROTEACEAE | |
| *Adenanthos flavidiflora* F. Muell. | *A. terminalis* R.Br. |
| *Lambertia multiflora* Lindl. | *L. formosa* Sm. |
| DROSERACEAE | |
| **Drosera rosulata* Lehm. | *D. whittakeri* Planch. |
| *D. menziesii* R.Br. | *D. planchonii* Hook.f. |
| MIMOSACEAE | |
| *Acacia cochlocarpa* Meissn. | *A. dallachiana* F. Muell. |
| *A. divergens* Benth. | *A. vomeriformis* A. Cunn. |
| **A. leptoneura* Benth. | *A. rigens* A. Cunn. |
| *A. pentadenia* Lindl. | *A. mitchellii* Benth. |
| PAPILIONACEAE | |
| *Bossiaea spinosa* (Turcz.) Domin | *B. foliosa* A. Cunn. |
| *B. peduncularis* Turcz. | *B. microphylla* Sm. |
| *B. rufa* R.Br. | *B. heterophylla* Vent. |
| *B. biloba* Benth. | *B. cinerea* R.Br. |
| *Chorizema genistoides* (Meissn.) C. A. Gardner | *C. parviflorum* Benth. |
| *Daviesia anceps* Turcz. | *D. alata* Sm. |
| *Jacksonia sternbergiana* Hueg. | *J. clarkii* F. Muell. |
| *Mirbelia ovata* Meissn. | *M. oxylobioides* F. Muell. |
| *Oxylobium microphyllum* Benth. | *O. cordifolium* Andr. |
| *O. tricuspidatum* Meissn. | *O. procumbens* F. Muell. |
| *Pultenaea spinulosa* (Turcz.) Benth. | *P. tenella* Benth. |
| RUTACEAE | |
| *Boronia alata* Sm. | *B. algida* F. Muell. |
| *B. crenulata* Sm. | *B. serrulata* Sm. |
| *B. penicillata* Benth. | *B. falcifolia* A. Cunn. |
| *B. viminea* Lindl. | *B. parviflora* Sm. |
| STACKHOUSIACEAE | |
| **Stackhousia pubescens* A. Rich. | *S. monogyna* Labill. |
| RHAMNACEAE | |
| *Spyridium complicatum* F. Muell. | *S. coactilifolium* Reiss. |
| STERCULIACEAE | |
| *Lasiopetalum acutiflorum* Turcz. | *L. ferrugineum* Sm. |
| DILLENIACEAE | |
| *Hibbertia gracilipes* Benth. | *H. billardieri* F. Muell. |
| *H. crenata* Andr. | *H. dentata* R.Br. |
| *H. inclusa* Benth. | *H. virgata* R.Br. |
| *H. mucronata* (Turcz.) Benth. | *H. acicularis* F. Muell. |
| THYMELAEACEAE | |
| *Pimelea preissii* Meissn. | *P. stricta* Meissn. |
| MYRTACEAE | |
| *Darwinia sanguinea* (Meissn.) Benth. | *D. micropetala* (F. Muell.) Benth. |
| *Eucalyptus calophylla* Lindl. | *E. gummifera* (Gaertn.) Hochr. |
| *E. ficifolia* F. Muell. | *E. intermedia* R. T. Baker |
| *Leptospermum erubescens* Schau. | *L. attenuatum* Sm. |
| *Micromyrtus drummondii* Benth. | *M. minutiflora* Benth. |
| EPACRIDACEAE | |
| **Leucopogon conostephioides* DC. | *L. rufus* Lindl. |
| **L. conostephioides* DC. | *L. deformis* R.Br. |
| *L. gilbertii* Stschegl. | *L. concurvus* F. Muell. |
| SOLANACEAE | |
| *Anthocercis microphylla* F. Muell. | *A. myosotidea* F. Muell. |
| GOODENIACEAE | |
| *Dampiera altissima* F. Muell. ex Benth. | *D. marifolia* Benth. |

This is believed to be the first published list of presumed vicarious species pairs between south-western and south-eastern Australia. Wood and co-workers (Wood and Baas-Becking 1937, Wood 1949 and Wood and Williams 1960) have compared the species occurring in dry sclerophyll forests of South Australia, New South Wales and the Australian Capital Territory, but their examples of supposed vicarious species pairs appear to be little more than representative species of the various genera, chosen without regard to systematic affinity or even total geographic range. Three species of *Acacia* which are quoted are *A. myrtifolia* (representing South Australia, even though it also occurs in the other regions), *A. discolor* (New South Wales) and *A. falciformis* (A.C.T.). One of these is bipinnate and the two phyllodineous species are not closely related systematically.

## Discussion

The present study has revealed the occurrence of geographically separated but systematically related populations in south-western and south-eastern Australia which show many different degrees of relationship. In some cases it has not been possible to differentiate the populations from the two areas, in others morphological differentiation has been at an infraspecific level, while further examples are given in which full specific distinctions are recognized, even though the populations are sufficiently similar to be considered true vicariads (i.e., presumably derived from an immediate common ancestor).

The existence of differentiated populations is most easily explained in terms of the Tertiary and Quaternary history of southern Australia, but in the case of discontinuous species in which the populations are morphologically indistinguishable it is felt that comparatively recent long-distance dispersal should be considered as a possibility.

It is likely that many of the species referred to above occupied former continuous areas which became broken up by the onset of unfavourable climatic conditions. Unfortunately, knowledge of the Australian flora of the upper Tertiary, Pleistocene and early Recent is scanty compared with that of the lower Tertiary. It is thought that the mid-Tertiary flora was a mesic one, that peneplanation was widespread and that the climate was humid and warm. Peneplanation was modified by vertical land movements beginning in the Miocene and culminating in the Upper Pliocene or Pleistocene, but the consequent climatic and edaphic changes are considered inadequate to explain the discrepancy between the distributions of Tertiary and present floras (Crocker 1959).

Crocker and Wood (1947) have suggested the existence of a Recent arid period, sudden and drastic enough to have had profound effects on a pan-Australian flora in the southern part of the continent. Their picture of the retreat of the pre-arid flora to refuge areas such as the Stirling Range, Mount Lofty Range, Grampians and Flinders Range is borne out by the present study of discontinuous species, many of which have been collected from two or more of these areas. Willis (1962) mentions several Grampians endemics "having undoubted Western Australian affinities." Crocker (1959) quotes the existence of "disjunct vicarious pairs, . . . major species disjunctions and the occurrence of relic species" as good evidence for the thesis of retraction and expansion.

Herbert (1929) quotes several species of *Eucalyptus* (e.g. *E. diversifolia* and *E. flocktoniae*) which are discontinuous between west and east, and suggests that their distribution is best explained by the onset of arid conditions in a previously well-watered central zone. He does not suggest a time for the climatic change.

Smith-White (1954) suggests that the areas of many species may have been simply bisected by the Miocene inundation of the Nullarbor Gulf, aided by a tract of arid country to the north, and that the bisection has been maintained to the present "in turn by physiographic, edaphic and climatic barriers".

Burbidge (1960) favours rather the late Pleistocene as the time of separation, on the basis of discontinuities between the two areas at the specific level.

The many degrees of morphological divergence between western and eastern populations may suggest that not all species were separated simultaneously. Stebbins (1950) points out that explanations in terms other than formerly continuous areas are possible, and mentions the possibilities of populations having always been separated although not to such a degree as at present and of the former existence of "stepping stones". The two extreme hypotheses (geological history and more recent long-distance dispersal) are not mutually exclusive, and combinations of the two are possible.

Overseas work on discontinuous species distributions has been summarised by Cain (1944). Most explanations have been based on past geological history, although often without direct fossil evidence. In some cases the discovery of fossil records from areas outside the living range of a species has given irrefutable evidence of contracting areas, but the necessary specific identification of the fossil specimens presents a formidable problem. In Australia we have no such records at the specific level which are likely to help elucidate west-east discontinuities. At the level of the subgenus, the occurrence of fossil leaves of corymbose eucalypts in Tasmania may point to the contraction of a former area occupied by a group of species, but gives no direct evidence at the specific level.

While geological history must be considered in explaining most discontinuities between south-western and south-eastern Australia, the possibility of propagules of certain species travelling long distances cannot be ruled out. Most objections to the general hypothesis of distance dispersal concern the establishment of propagules in a foreign environment, in competition with local species. Turrill (1959) has mentioned the ability of polyploids to extend into habitats unfavourable to their diploid progenitors but cautions against the drawing of broad conclusions. The role of vegetative reproduction as an aid to establishment is discussed by Baker (1953), and facultative apomixis could well be important. Taylor (1955) has discussed the establishment of alien species under natural conditions on Macquarie Island.

The instances of *Eucalyptus cladocalyx* and *E. ficifolia*, whose natural ranges are much smaller than in cultivation, may indicate a low capacity for dispersal or establishment, although these distributions may be of "young" species which have not had time to occupy all available habitats.

It will be noticed that a high proportion of orchids occurs in the list of discontinuous species set out above. Seeds of *Microtis atrata* were measured and found to be about 200 x 65 $\mu$ while those of *Thelymitra flexuosa* were about 180 x 100 $\mu$. The smallest non-orcidaceous seeds were those of *Levenhookia pusilla* (about 500 x 220 $\mu$). There seems no reason why seeds of this magnitude should not be carried long distances in the atmosphere. Ridley (1930) quotes examples of mineral particles 1/200th in. (1,270 $\mu$) diameter being identified 970 and 600 miles from their respective sources and concludes by saying that "dust seed (Orchidaceae) . . . may travel a distance of as much as 700 miles" in one flight. Taylor (1955) suggests that species with very small seeds may have arrived on Macquarie Island as a result of wind transport, quoting as evidence the discovery of pollen grains of *Podocarpus* 600 miles from their nearest source of supply. Small (1921) quotes an experiment in which it was found that a light breeze of about two miles per hour is sufficient to support a dandelion fruit in the air indefinitely.

Accepting for the moment the possibility of wind dispersal having operated between south-western and south-eastern Australia, there is no climatological information to suggest the more likely direction. According to Kendrew (1937) and Gentilli (undated), southern Australia is characterised by prevailing winds in a general westerly direction in summer and easterly in winter, but there is much day to day variation. It is often assumed that the south-western region served as a centre of origin of many autochthonous species, on the basis of the high proportion and number of endemic genera found there.

There do not appear to be any well defined animal migration routes which could have carried propagules between the two areas in recent times. Aborigines are not likely to have carried seed deliberately for any distance although it is suggested that accidental carriage by aborigines may have occurred during their 8,000 year occupancy of Australia. Alternatively, early human occupants of this country may have disturbed the habitat sufficiently to create favourable conditions for the establishment of alien propagules carried by long distance wind dispersal.

With regard to the vicarious species, the main problems are the verification of true systematic affinity between the members of each pair, and the determination of whether the species are true or false vicariads. Löve (1954) has applied cytotaxonomic studies to corresponding types from North America and Europe and has shown 92 pairs of truly vicarious taxa and 41 pairs of substitution species, having different chromosome numbers. He has found that both vicarious and substitution types are to be found at different stages of separation, from habitat separation in the same region to physiographic or historic separation in different regions.

It is envisaged that future investigations will be undertaken in the following stages, with a view to obtaining further information relative to the foregoing observations:

(i) Field collection of material for detailed comparison of morphology, anatomy, cytology, breeding systems and habitat preferences (the information so far collected from herbarium labels has proved too scanty to provide useful comparisons of habitats).

(ii) Investigation of survival of small seeds in the laboratory under conditions of temperature and humidity likely to be encountered on a transcontinental journey.

(iii) Cultivation and crossing of western and eastern individuals, in order to obtain some measure of genetic divergence.

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Volume 47 1964

Part 1

## Contents

1.—The Environment of the Quokka *(Setonix brachyurus)* in the Darling Range, Western Australia. By G. M. Storr.

2.—An Ordovician Cystoid (Pelmatozoa, Echinodermata) from Western Australia. By Ida A. Brown.

3.—Description of a new Stonefish of the family Synaceidae from Western Australia. By R. J. McKay.

4.—Association of Larger and Planktonic Foraminifera in single samples from Middle Miocene sediments, Guadalcanal, Solomon Islands, south-west Pacific. By P. J. Coleman and R. A. McTavish.

5.—Discontinuous and Presumed Vicarious Plant Species in Southern Australia. By J. W. Green.

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# 6.—The Woolgorong Stony Meteorite

By G. J. H. McCall[*] and P. M. Jeffery[†]

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Numerous fragments of a stony meteorite were recovered from Woolgorong Station, north-north-east of Mullewa, Western Australia and approximately 300 miles north of Perth in July, 1961, and later in the same year. This find almost certainly represents a possible fall noted in this locality in December, 1960. A double report was heard at this time, but the authors consider that this does not necessarily imply a multiple fall since phenomena of this kind are generally attributed to compression wave effects high in the atmosphere. The meteorite is a veined and brecciated, grey hypersthene-olivine chondrite, Prior's class III, and shows evidence of pronounced recrystallisation. Recovery of fragments from shallow burial in the soil and from the surface, has allowed a confident reconstruction to be made. There is evidence that it had an aerodynamically stable form under conditions of atmospheric entry, since surface patterns and the distribution of thickened and thinned fusion-crust reveal a distinct orientation. Such orientation supports the idea that this was a single fall, complicated only by fragmentation at or near the point of impact.

Microscopic study has revealed considerable structural variation, some areas revealing well-formed, though recrystallised, chondrules. Others show almost complete recrystallisation to a granular aggregate of polysomatic and larger fractured grains. In these areas of recrystallisation the chondrular structure is only vaguely defined.

Chemical tests, etch-tests, X-ray diffraction studies and two full chemical analyses have been carried out, and the results are given here. The minerals determined include kamacite, iron sulphide (troilite?) olivine (chrysolite-hyalosiderite), orthopyroxene, oligoclase, and possibly a calcium silicate (rankinite?).

## Introduction

In August, 1961, the report of a possible meteorite discovery reached the Geological Survey of Western Australia (Lord, unpublished data). The report came from Mr. F. R. Wickman, Manager of Woolgorong Station (Fig. 1), the site of the discovery (latitude 27° 43′ S, longitude 115° 50′ E).

This discovery followed seven months after the experience of unusual phenomena including sounds normally associated with explosions, heard by people at or near the Station. Even at that time the possibility of a meteorite fall was discussed, though the possibility that an aircraft in distress was involved was also suggested, and indeed an air search is reported to have been initiated. The meteorite was recovered as a direct result of attempts to locate the object which had caused this disturbance.

The detailed investigation of this fall was passed over to the Director of the West Australian Museum, Dr. W. D. L. Ride, and he visited the site of the find with Mr. D. Merrilees later that year, recording details of personal impressions of the 1960 phenomena and examining the traces of the fall. They collected further fragments of the stone, in addition to those originally collected by Mr. A. J. Noldart of the Geological Survey of Western Australia (Lord, unpublished data).

At the request of Dr. Ride, the investigation has been supervised in its later stages by honorary associates of the Museum, members of the Meteorite Advisory Committee which acts in an advisory capacity to the Trustees of the Museum; Dr. McCall, who has supervised petrographic and chemical investigations, and compiled the information here given concerning details of the fall and external features of the meteorite; and Dr. Jeffery who has carried out X-ray diffraction studies. The actual chemical analysis was carried out at the British Museum (Natural History), London: an additional X-ray diffraction determination was also carried out at the British Museum (Natural History).

This meteorite was initially supposed to be achondritic—if this was correct it would have been an exceedingly rare occurrence; however, access to the whole collection of recovered fragments showed that initial microscopic studies had been carried out on a very strongly recrystallised area within the stone, an area showing little trace of rounded chondrules, and that the bulk of the fragments show distinct, rounded chondrular insets. While the find is not as rare as was at first suspected, the amount of material recovered, the diverse internal texture and structure, and the excellent preservation of external features characteristic of oriented meteorites, make this one of the most interesting meteorite finds in this State.

## History of Fall and Reconstruction of Meteorite

### Discovery of the Meteorite

In July 1961, Mr. W. Hamlet and Mr. C. Monger both employed at Woolgorong Station, unearthed what they called a "sky stone" at a point situated a few hundred yards north-west of the Station homestead. A shallow crater some twelve inches deep had been formed in the

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topsoil, and the mass had apparently disintegrated into angular fragments on impact. The manner in which the crater was gouged into the soil suggested (to those who have visited the site) impact at a reasonably shallow angle of incidence, and no abnormal velocity, on a flight bearing of 320°—that is, close to north-west. The preservation of a trail of small meteorite fragments and dust along the same trend line supported this conclusion. Some larger fragments were collected up to three feet from the small crater, perhaps due to rebound on impact. The geologist of the Geological Survey of Western Australia who first visited the site reported that the site of the fall was a broad, flat plain of red soil, which overlies a thick, indurated crust of the type locally known as the "Murchison Cement."

### The Reported Fall

It must be borne in mind that all the reports bearing on the phenomena observed in December, 1960, were made to Dr. Ride and Mr. Merrilees a year later. However, they correspond so closely with other descriptions of meteorite falls, contained in the literature, that there seems no reasonable doubt that the meteorite fell at this time.

As is not uncommon, auditory effects predominated—the only visual observation recorded being a slight haze or dust cloud noted by Mr. F. R. Wickman, who was at the homestead on the afternoon shortly before Christmas, 1960 (Dec. 20th?) and at about 1400 hours heard a swishing noise followed by a dull bang "like a couple of plugs of gelignite going off forty feet underground." The suggestion of two distinct reports, one at Woolgorong and one to the north-north-west, towards Yallalong (Fig. 1) is present in several recorded descriptions of this event. At Yallalong a noise was heard which suggested that an aircraft was in distress, and it is said that a light aircraft actually took off to search for it. Though this record of a double report could mean a double fall—meteorites do, in fact, usually fall in multiple associations rather than as single bodies—such sound effects are more commonly attributed to compression waves high in the atmosphere, as the still speeding meteorite enters the atmosphere and commences to decelerate (an effect akin to the supersonic bangs of jet aircraft). The evidence of orientation (p. 38) suggests that this was in fact, a single fall up to the point of fragmentation at or near contact with the ground. If a second stone does exist, the nature of the terrain and the rapid deterioration of stony meteorites are factors likely to preclude further recovery.

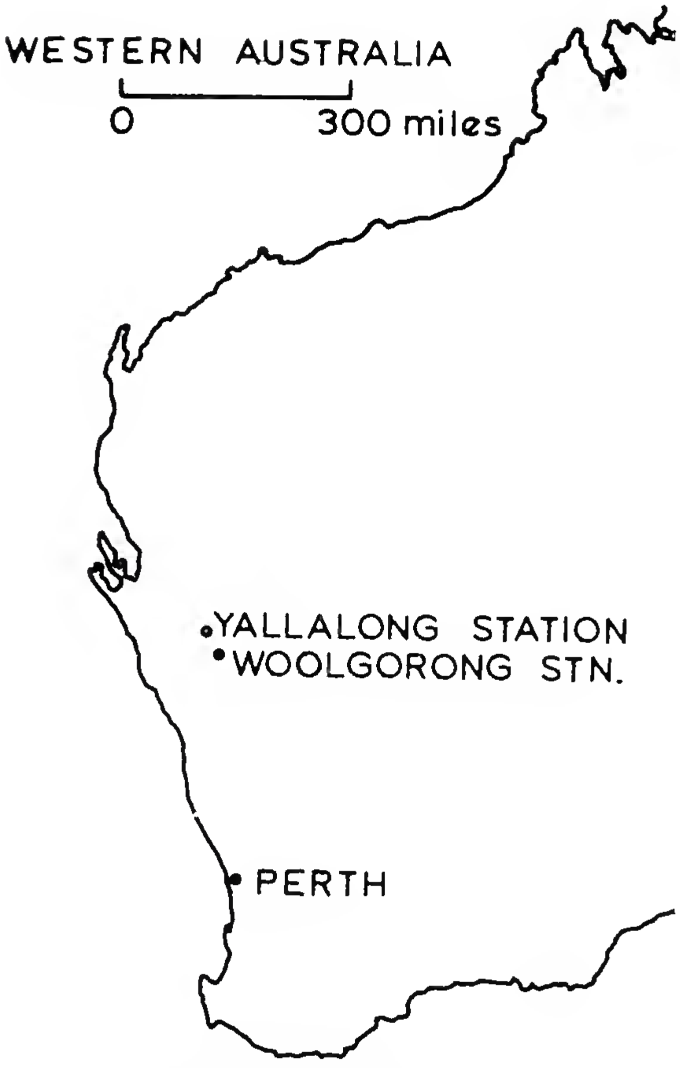

Fig. 1.—Sketch map showing the position of the Woolgorong fall and meteorite recovery.

The reports were heard up to thirty miles from the homestead at Woolgorong, and this in itself supports the idea that the sound effects were due to shock-waves—it is unlikely that the report produced on impact with the earth of a mass of about one hundred pounds weight could ever be heard so far from the point of impact. Stones of this size reach the surface of the earth at a velocity in no way comparable with their velocity through space because of the effect of atmospheric braking, and the shallow and partial burial of this meteorite testifies to impact at a velocity probably not far off, or at, the speed of free fall: the close association at the site of the find of the fragments which were later pieced together with perfect interlocking junctions testifies to very late fragmentation, probably on impact, though the cracks had clearly started to form before this time.

Mr. Hamlet recalls a loud report and a noise like a thunderstorm, but saw no flash; Mrs. Wickman likened the noise, again, to an aircraft in difficulty, and believes that a short (but appreciable) pause separated the two reports.

### The Meteorite Fragments

A total weight of about eighty pounds of fragments has been recovered. Of these the bulk, comprising five large and numerous smaller fragments are held at the West Australian Museum (W.A.M. No. 12113 a, b and c).* Another large, fusion-crust coated fragment, weighing 7½ lb., was retained at Woolgorong Station.

Two small fusion-crust coated fragments are held in the collections of the Geological Survey of Western Australia and the Government Chemical Laboratories. Another such fragment has been supplied to the Keeper of the Mineralogical Collections at the British Museum (Natural History).

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* Some of the material collected was temporarily stored in contact with galena samples. Any geochemical work on trace element content should therefore be restricted to specimens marked 12113b which are not so contaminated.

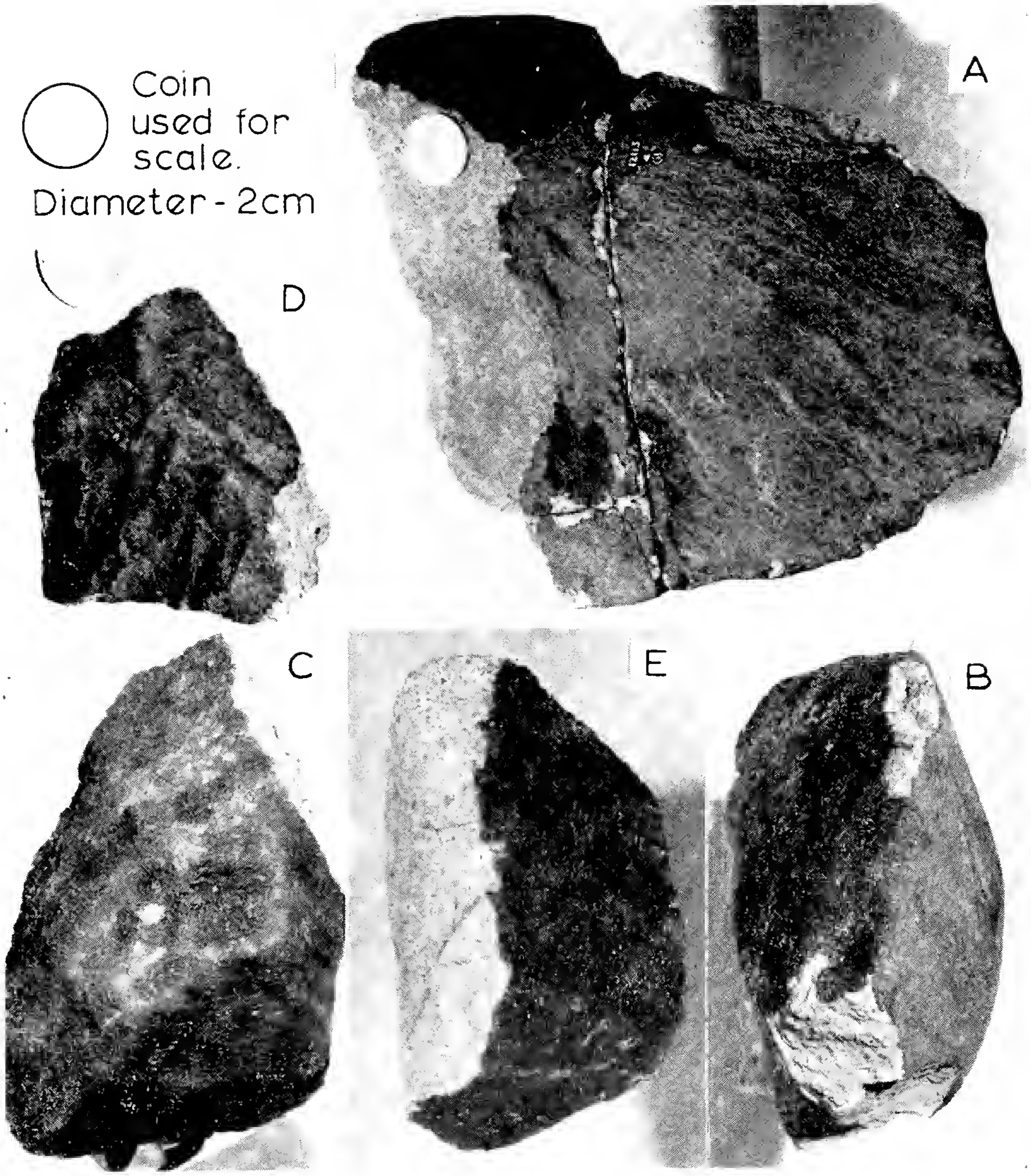

Plate 1. A. Some larger fragments fitted together to reassemble the entire termination of the original mass (eight fragments can be fitted together exactly, but an assemblage of only four is shown here). The thin, brown fusion-crust which covers the surface contrasts with a grey, freshly-broken surface revealed on the left hand side of the photograph. This surface is believed to be the anterior surface. Radiating striae and regmaglypts show clearly on the surface of fusion-crust (coin indicates scale).

B. End-on view of the same reconstructed termination showing contrasting fusion-crust surfaces, the posterior surface in atmospheric flight being rough, blackened and thickened (scale as above).

C. Facetted fragment from the opposing termination of the original mass (scale as above).

D. Fragment showing elongated regmaglypts.

E. Fragment showing the thickened fusion-crust of the posterior surface, contrasting with that shown in Plate 1 A above (X ½).

The fragments show mostly freshly-fractured surfaces, appearing grey with patches and streaks of iron oxide staining, and are of moderately coarse grain. Specks of metal punctuate these broken surfaces, appearing glistening and of grey to brown colour on faces freshly cut with the diamond saw, but rapidly tarnishing to the brown colour seen on all the faces opened up at the actual time of fragmenation. Thin, thread-like veinlets traverse the stone; most are infilled with glassy material, projections of the fusion-crust inwards at the time of incipient fragmentation (Plate 1E). These are apparently what Krinov (1960, p. 190) calls "surfaces of the second kind," which develop only during the final stage of progress of the meteorite through the atmosphere. There are, however, some veinlets infilled with sulphide (p. 38) and these veinings must be due to some process which occurred long before the brief transit of the stone through the terrestrial atmosphere—a process which presumbly occurred within the parent planetary body.

Rounded chondrules show clearly on some broken surfaces: some are up to half a centimetre in diameter, and most of them are composed of ferromagnesian silicates showing bluish-grey within the lighter grey granular base, and not apparently aggregated with any metal or felspar. Metallic chondrules of similar rounded shape are not numerous, but can be recognised; some form solid metallic pellets up to half a centimetre in diameter but most are of considerably smaller size. In the granular base, which forms considerable chondrule-free areas and encloses the chondrules where these are manifest, creamy-white specks of felspar can be recognised.

Some fracture surfaces show a brecciated appearance, due to the presence of insets of irregular form, appearing as angular fragments (Plate 2B)—these are mostly broken or partly recrystallised chondrules, but some seem to be simply fragments of varying texture—it is however, essentially a monomictous breccia in that all the fragments stem from a single type of stony meteorite.

The fusion-crust is evident on many fragments; it shows a pronounced variation in thickness and character, the thickness ranging from less than 0.5 mm. to more than 0.75 mm., and the areas of thickening (Plate 1E) being characterised by a noticeably roughened surface, black in colour and traversed by a fine network pattern of polygonal shrinkage cracks, the diameter of the polygons being in the order of half a centimetre. In contrast, the fusion-crust shows in the areas of thinning (Plate 1), a smoother surface and a brownish colouration; striations are here more in evidence, but polygonal shrinkage cracks less so. Perfect thumb-print regmaglypts are sparsely indented in the fusion-crust (Plate 2C); the regmaglypts at the border area of the thinned crust, near the sharp coigns in the facetted meteorite (Fig. 2), are however, almond-shaped, and elongated parallel to the finer striations on the glass surface (Plate 1A, D). According to the accepted theory, the circular thumb-prints appear where there is little ablation while the elongated regmaglypts appear where ablation results in strongly linear flow effects. Striae are present on both thickened and thinned areas of fusion-crust, but are far less evident on the rough, black, thickened areas of fusion-crust (Plate 1C) as are shallow regmaglypts.

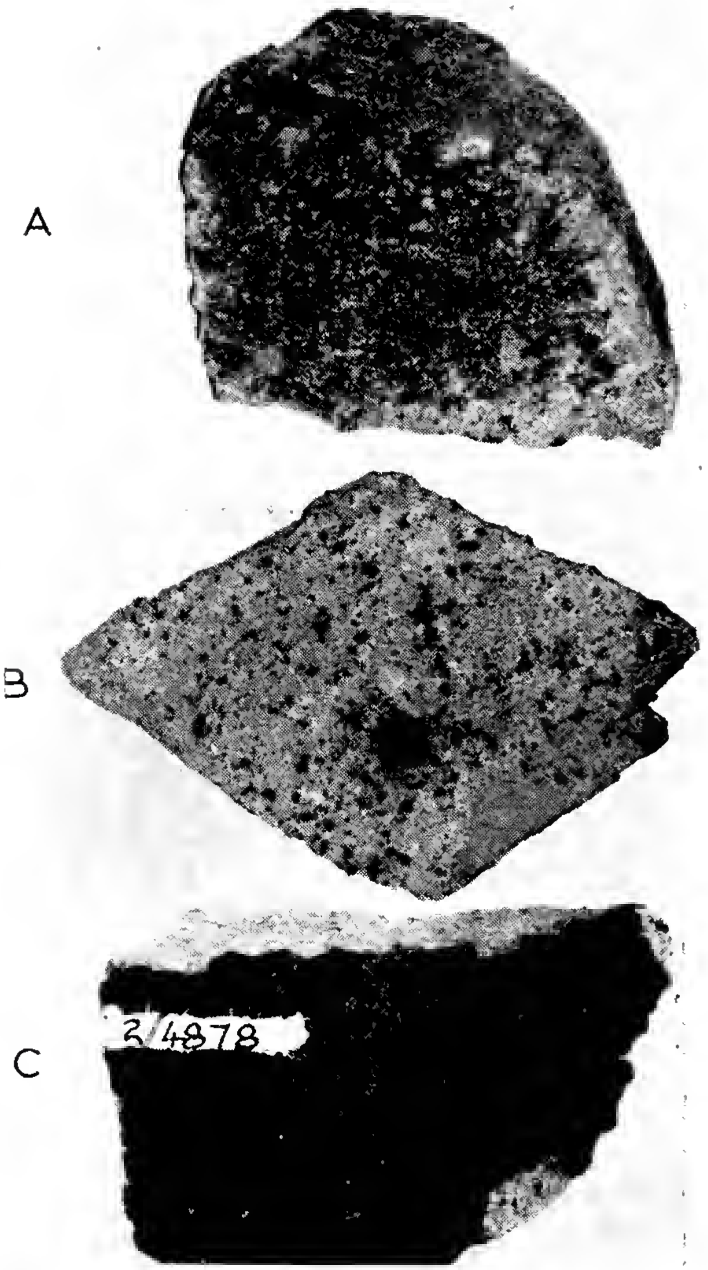

Plate 2. A. Fragment showing a glass-veneered surface due to the fact that the meteorite has fractured along a plane of fracture of the "second kind" (p. 36) (X ½).

B. Cut face of a fragment showing circular and angular chondrular insets of ferromagnesian minerals, giving to the meteorite a brecciated character. The arrangement of the nickel-iron and sulphide along stringers is evident, and there is one large, wholly-metallic chondrular inset (scale, width of the specimen is 2½ inches).

C. Thumb-print regmaglypts (scale X 1.25).

## Reconstruction and Orientation

It has not been possible to fit together all the available fragments so as to reconstruct the entire mass, enclosed by fusion-crust, as it was before fragmentation. However, it is probable that at least two-thirds of the mass is represented by fragments held in known collections. The difficulty arises due to the small size of many of the fragments and the fact that a portion from the middle of the mass seems to be not represented by any large fragments. A single termination comprising about one-third of the original mass was successfully reconstructed, the various pieces, numbering eight in all, being joined on tightly-interlocking faces. The reconstruction of four of the largest fragments into this termination is shown in Plate 1A. This reconstruction of one termination of the mass allowed a confident estimation of the length and cross-section shape of the stone, by means of extrapolating the very regular curvature of the faces of this part of the mass. The total length of the mass was probably not more than three feet, the maximum width just over twelve inches, and the maximum depth six to seven inches. The probable shape of the original mass is shown in Fig. 2, together with the fusion-crust patterns.

A fortunate chance in the correspondence of a set of striations and the nature of the crust on the surface of one large fragment with those on the thickened surface of the reconstructed termination, allowed this fragment to be identified and orientated as the opposing termination of the boat-shaped mass. This fragment, shown in Plate 1 C, is drawn in its probable position in Fig. 2. It seems that one termination was spatulate while the other was facetted, and the lateral margins of the flattened boat-shaped mass were also different, one being continuously curved while the other had a steeply-facetted form and was bounded by abrupt coigns.

The pattern of striations, regmaglypts and fusion-crust thickening suggests that this mass had an aerodynamically-stable character while travelling through the atmosphere—that is, it

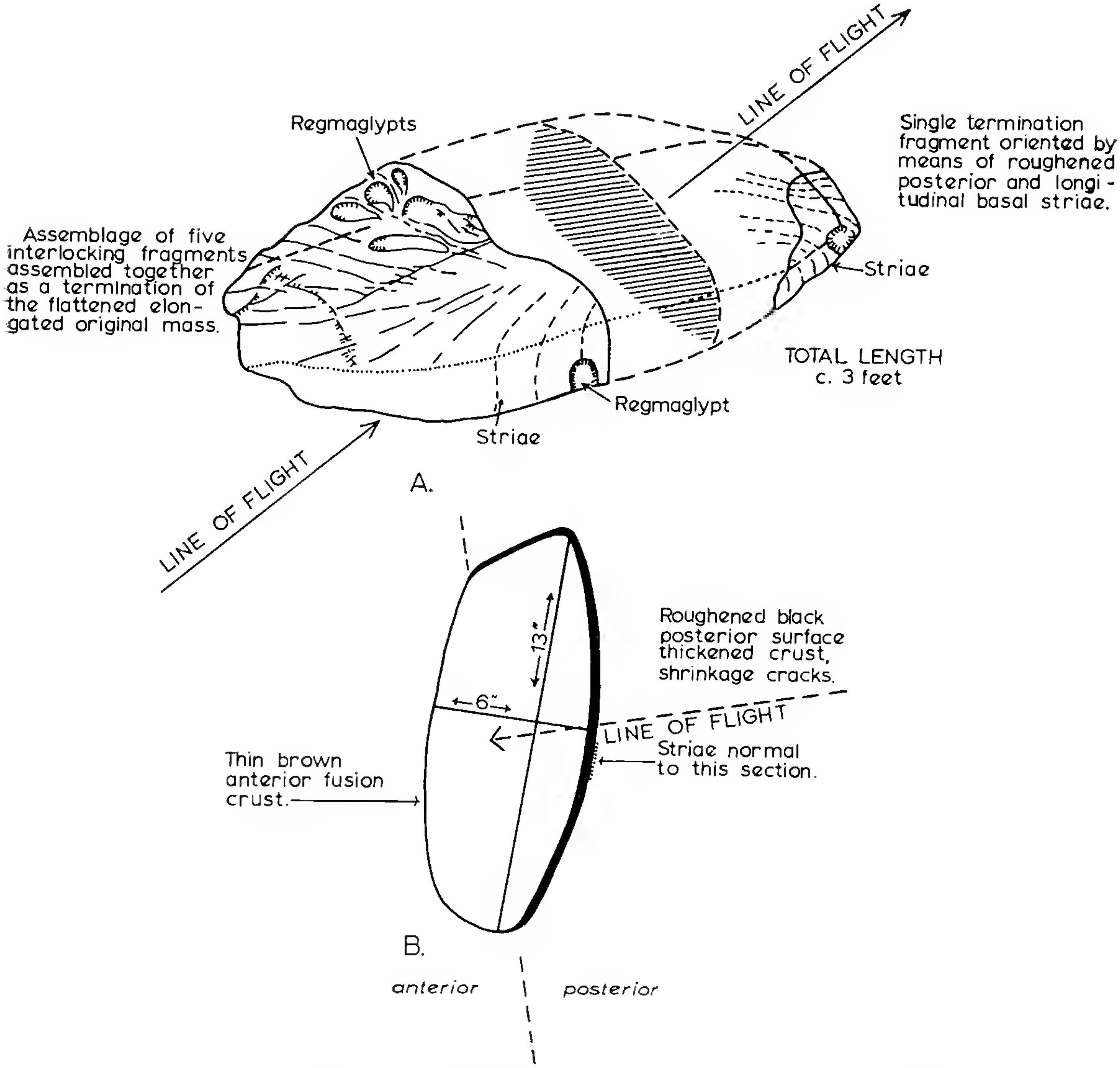

Fig. 2.—Diagrammatic reconstruction of the probable form of the original mass before fragmentation, showing surface patterns and their probable relationship to the attitude adopted by the mass while in atmospheric flight. The cross-hatched plane represents a cross-section of the meteorite.

did not rotate to any extent. This means that it is an orientated meteorite; such a character is somewhat unusual, and is supposed to be evinced by meteorites which have entered the atmosphere as a single mass, and not suffered fragmentation until impact or the very last stage of their transit through the atmosphere. The probable flight attitude is shown in Fig. 2, and the extreme anterior point was probably situated near to the coin, shown to give the scale in Plate 1 A. In spite of the evidence of orientation, the mass does not seem to have been symmetrical.

## Petrography

### The Metallic Fraction—Megascopic Details

The metallic fraction occurs as grey to brownish specks, stringers and pellets within the stone, and is mostly fringed by hazy, brown iron oxide discolouration of the surrounding silicate minerals. It forms between 10 and 15 per cent. by volume. One large pellet, half a centimeter in diameter was removed bodily, etched with 8 per cent. HNO$_3$, and tested for nickel and sulphide. Etching revealed a coarse irregular pattern (Fig. 3), clearly not an organised octahedral Widmanstatter pattern. The possibility that this pattern could stem from aggregation of the sulphide within the metallic areas is suggested. That considerable sulphide is present was shown by dissolving some of the metal in concentrated HCl, H$_2$S fumes being evolved (troilite dissolves in this way); and the reaction with dimethylglyoxime gave a strong pink colouration indicative of nickel.

X-ray diffration studies (p. 42) provided confirmation of the tentative recognition of the principal metal component as kamacite, and the absence of taenite revealed by these studies confirmed that the etch-pattern could not be an octahedral Widmanstatter etch-pattern.

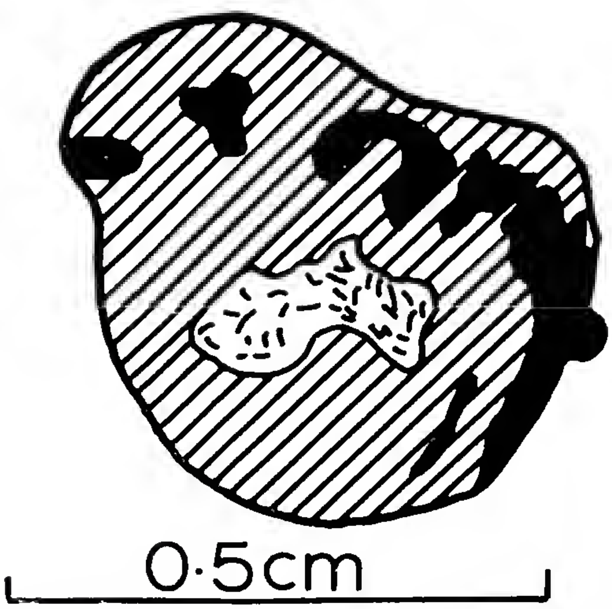

Fig. 3.—Irregular etch pattern developed after etching the cut and polished surface of a large metallic pellet (Plate 2 B) with 8% HNO$_3$. The cross-hatched area is kamacite, the black enclaves are etch-pits, probably reflecting sulphide inclusions within the nickel-iron. The central area is a deep cavity produced on etching—its origin is uncertain.

### The Silicate Fraction—Megascopic Details.

The silicate minerals of meteorites tend to present unfamiliar surface appearances to the petrologist familiar with terrestrial olivine, pyroxenes and felspars. In this meteorite the felspars have the usual creamy-white colour, but the light grey colour of the olivine, and the bluish colour of the ferromagnesian minerals of the chondrules are atypical of terrestrial olivine and orthopyroxenes. The finely-shattered or finely-granular nature of the crystals which is apparent on microscopic examination, probably accounts for this unusual appearance in the hand-specimen. The metal-free and felspar-free character of some chondrules is very noticeable, as is the fact that micro-faulting within the stone has displaced portions of some chondrules relative to the remainder. This, together with the angular and fragmental nature of some chondrules accounts for the brecciated appearance seen in certain areas of the meteorite (Plate 2 B). The light grey colour of the bulk of the silicate fraction, together with the more bluish-grey colour of the chondrules leave no doubt that this should be classified as a grey chondrite (in the older terminology of Brezina), and the structure noted above requires the addition of the term brecciated.

### The Metallic and Silicate Fractions—Microscopic Examination

Under the microscope, the meteorite reveals a predominant content of transparent silicate minerals and subordinate opaque nickel-iron. It is almost free from glass, except for fusion-crust and extensions of it into cracks. The metal percentage is below the upper limit of metal content of aerolites and thus no other appellation can reasonably be given. The silicate minerals are:—

Olivine (var. chrysolite—hyalosiderite)
Orthopyroxene (enstatite-hypersthene)
Plagioclase felspar (var. oligoclase)

Plate 3. A. Photomicrograph. Finely granular chondrule composed largely of orthopyroxene (dark-grey). Felspar (white) and metal (black) fringe the chondrule and stringers of this material tend to terminate at its margins. Vague fan structure is recognisable (X 63, Plane polarised light).

B. Photomicrograph. Another such chondrule, but mainly composed of olivine. It shows similar fringing crystallisation of nickel-iron and sulphide (black) and felspar (white), but here the minerals seem to have "eaten" into the chondrule at its margins, probably in the course of the partially completed process of recrystallisation. Troilite (black) occurs in a veinlet on the right hand side of the photograph, a veinlet of the type that occasionally transects the chondrules (X 63, Plane polarised light).

C. Photomicrograph. A grated chondrule apparently entirely composed of olivine lamellae without associated glass; clearly strongly recrystallised (X 125, Plane polarised light).

D. Photomicrograph. An exocentric fan chondrule, apparently entirely composed of olivine (X 63, Plane polarised light).

E. Photomicrograph. A microporphyritic chondrule consisting of sulphide (black), felspar (white) and dark, dusty aggregates of cryptocrystalline material or glass; this chondrule appears as if partial assimilation has occurred during the recrystallisation process (X 100, Plane polarised light).

F. Photomicrograph. A fan chondrule of cryptocrystalline material or glass (cloudy black), sulphide (black) and felspar (white). Olivine shows as grey granules (X 100, Plane polarised light).

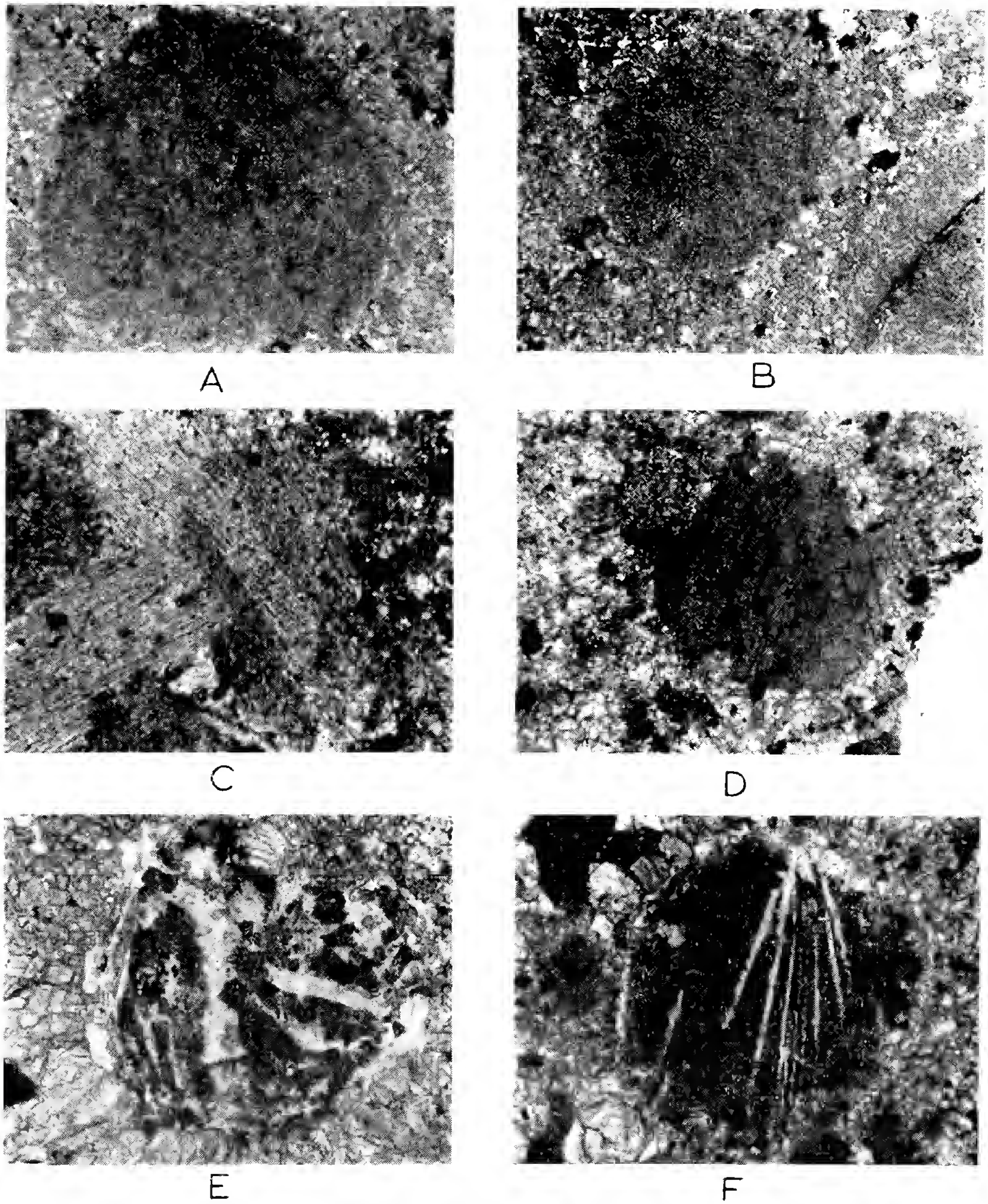

PLATE 3

No other silicate minerals could be optically determined.

*Olivine.*—Entirely fresh, it shows some evidence of subhedral form in "gabled" terminations of some larger grains, but is mostly anhedral. It may be of somewhat fibrous appearance in the chondrules. Irregular granules tend to show a polysomatic character, being granulated into innumerable minute granules bounded by planes of cleavage and parting within the larger crystal (Plate 4 A, B). The granulation has locally proceeded so far that the granulated aggregates of minute grains bear no trace of the larger grains from which they have been derived. As the dominant silicate mineral, olivine occurs in both chondrules (Plate 3 C, D) and areas of almost complete recrystallisation devoid of apparent chondrules (Plate 4 A): it is evident in the lamellae within grated chondrules (Plate 3 C).

The diagnostic optical characteristics are an interference figure indicating a biaxial mineral with a very large optic angle (c.80°) and a negative sign, and refractive index values ranging from 1.68 to 1.72. These properties fit in with a slightly ferroan variety, compositionally slightly towards the hyalosiderite range from chrysolite ($Mg_{80}Fe_{20}$). This agrees with the chemical determination as probably c.$Mg_{75}Fe_{25}$ (p. 41). This is the typical olivine of Prior's Class III, hypersthene-olivine-chondrite.

*Orthopyroxene.*—This can be recognised in thin sections on account of better cleavage and lower birefringence than the olivine. It is, however, often difficult to differentiate in fine grains. Present in both chondrules and areas of almost complete recrystallisation, it is of a non-pleochroic variety. The optical sign seems to be negative (though few good interference figures were obtained) and the most probable identity is hypersthene lacking pleochroism. Deer, Howie and Zussman (1963, p. 30) state that in orthopyroxenes the pleochroism is not a factor of increasing iron content but is independent of the Mg0/Fe0 ratio, and thus non-pleochroic, ferroan orthopyroxenes are not unknown. It must, however, be noted that while enstatite is ruled out as a modal component on account of the chemical evidence (p. 41), modal bronzite is possible since Prior's classification (1922) is chemically based and involves assessment of the Mg0/Fe0 molecular ratio in all the

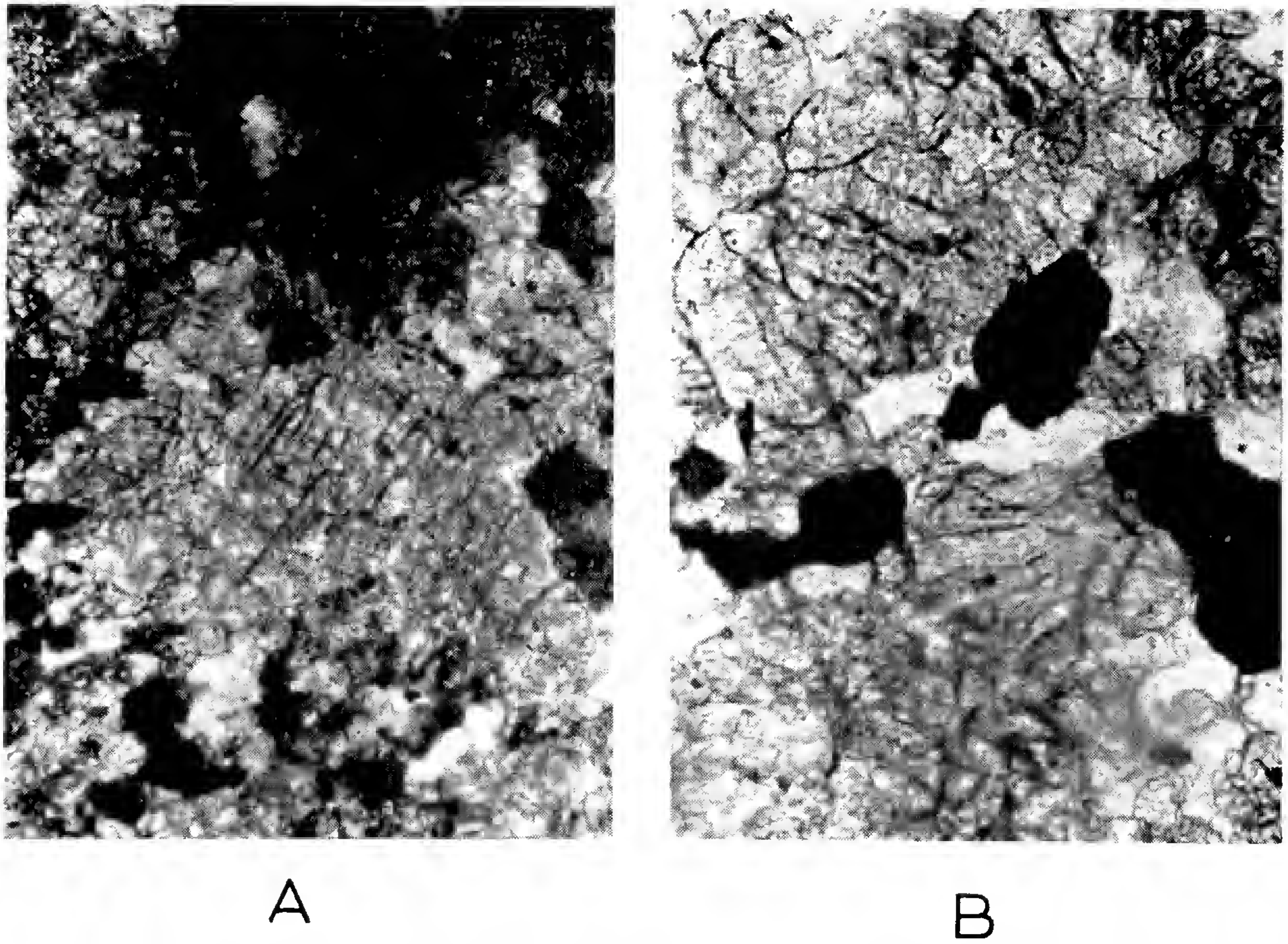

Plate 4. A. Photomicrograph. A strongly recrystallised area of the meteorite. The finely cracked, polysomatic nature of the olivine grains (grey) is apparent, as is the manner in which the felspars (white) are aggregated interstitially and along stringers with nickel iron and troilite (black) (X 163, Plane polarised light).

B. Photomicrograph. A similar recrystallised area under higher magnification. Kamacite shows black, olivine grey, and oligoclase felspar white. The texture of this area of the meteorite appears not dissimilar from that of many terrestrial igneous rocks (X 320, Plane polarised light).

silicate fraction, while in fact olivine tends to take up rather more iron in proportion to magnesium than orthopyroxene (Prior and Hey, 1953, p. x).

*Plagioclase.*—Present as colourless interstitial granules, translucent and showing distinct cleavage but only seldom showing lamellar twinning, the felspars are quite fresh. Refractive index determinations and measurements of the extinction angles on a few recognisable lamellar-twinned grains indicated that it has the composition of oligoclase, somewhere between $An_{20}Ab_{80}$ and $An_{25}Ab_{72}$, slightly more sodic than the theoretical deduction of $An_{40}$ (andesine) from the normative calculation.

Modal analysis is not entirely satisfactory because of the difficulty of differentiating between fine grains of pyroxene and olivine, and the variability of the material. The following would, however, seem to be a fair approximate assessment of the mode:—

Metal. Nickel-iron (kamacite) + sulphide (troilite) 10 - 15

Silicates. Ferromagnesian (olivine + hypersthene) 80±

Oligoclase 3 - 10

Microscopic study using reflected light allowed a clear distinction between kamacite and troilite. The later developed veinlets are entirely of sulphide. Bright reflectant specks aggregated with the kamacite may be schreibersite.

### Texture and Microscopic Structure

The texture and structure are very variable. Chondrules provide the most striking structural feature; these mostly show well-rounded shapes (Plates 3 A, B) but some are broken, and some appear to have been partly absorbed in the recrystallised containing mass, again losing their regular shape. The grated chondrules show no evidence of ever having possessed any regular shape (Plate 3C). In the strongly recrystallised areas the chondrular structure is often not apparent. The range of internal textures is that normally associated with chondritic aerolites; the granular type called microporphyritic, the fan forms showing an exocentric focus (Plate 3 D), and grated chondrules are all abundant, but monosomatic (single crystal) chondrules have not so far been recognised. Felspar and metal are absent from most of the chondrules. There are sparse metallic chondrules, either composed entirely of metal or of sulphide and cryptic isotropic material (glass?) associated with felspar (Plates 2 B, 3 E, F); the latter include both microporphyritic and fan forms.

The relationship of the felspar and nickel-iron (native metal and sulphide) to the ferromagnesians and to the chondrular insets is one of the most interesting features of this meteorite. In recrystallised areas both nickel-iron and felspar are interstitial to the ferromagnesian grains (Plates 4 A, B); often this interstitial growth is arranged in narrow stringers and there are very well defined veinlets of the same material (Plate 3 B). These stringers tend to terminate in peripheral fringes around the chondrules (Plates 3 A, B), but rare examples, such as that shown in Plate 3 B, cut through them. The relationship suggests a late mobilisation and introduction of nickel-iron (+ sulphide) and felspar into a chondrite showing only very limited development of these minerals in the form of sparse chondrules. There seems to be some evidence of the same fringing relationship of sulphide and felspar to sulphide/felspar/glass chondrules as seen in the silicate chondrules, and these too seem to have been early structures which have been later invaded by material identical with that which composes them. The alternative interpretation—that the sulphide/felspar chondrules represent crystallisation in spheroids from these stringers seems unlikely. Lovering (Moore, 1962, p. 195) has suggested a sequence of genetic phases in meteorites, and this felspar-metal invasion which seems to accompany recrystallisation seems to fit in well with this concept.

The classificatory terms of the older Brezina system, veined and recrystallised (crystalline), seem entirely justified by the structural and textural evidence.

The texture and mineralogy of the recrystallised areas (Plates 4 A, B) of this meteorite would be difficult to differentiate from that of some ultrabasic igneous rocks were it not for the presence of nickel/iron with subordinate sulphide rather than entirely combined in ore minerals—oxides and sulphides characteristic of such rocks. This comparison could well have a petrogenetic significance, in respect of the derivation of crustal igneous rocks from the mantle.

### Chemical Analysis

Two full chemical analyses have been carried out on specimens chosen at random from the collection at the West Australian Museum. The only selective factor was that specimens of fresh appearance were chosen.

Before sending the specimens for analysis a set of specific gravity determinations was made on five of the fragments. The results obtained were 3.45, 3.46, 3.53, 3.54, 3.58; *Average* 3.51.

Results of analysis by Dr. A. A. Moss, British Museum (Natural History) are as follows:—

Analysis by the Method of Prior (1913).
Lab. No. 2943.

*Percentage Composition*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Fe | 6.31 | $TiO_2$ | 0.10 | MnO | 0.29 | $Na_2O$ | 1.04 |
| Ni | 0.99 | $Al_2O_3$ | 2.98 | FeO | 14.07 | $K_2O$ | 0.14 |
| Co | 0.05 | $Cr_2O_3$ | 0.54 | MgO | 24.88 | $H_2O+$ | 0.04 |
| FeS | 6.43 | $P_2O_5$ | 0.09 | CaO | 1.89 | $H_2O-$ | 0.09 |
| $SiO_2$ | 39.95 | | | | | | |

*Total* 99.88%

*Normative mineral composition*

| | |
|---|---|
| Olivine (close to $Mg_{1.5}Fe_{0.5}SiO_4$) | 46.94 |
| Bronzite* | 25.19 |
| Felspar† | 12.69 |

* The conversion of a meteorite analysis by Prior (1913) to normative values involved the allocation of excess $CaSiO_3$ to bronzite, a mineral that does not contain any calcium silicate. This seems without any real basis and it would perhaps be better to express the $CaSiO_3$ excess simply as $CaSiO_3$. However, in conformity with the accepted practice, the figure for bronzite given here includes $CaSiO_3$ excess: it must be noted that this will make the bronzite value somewhat higher than the expected modal orthopyroxene content.

† The felspar normative values are Or .84, plagioclase remainder (c.$An_{40}Ab_{60}$).

| | |
|---|---|
| Ilmenite | 0.18 |
| Chromite | 0.81 |
| Apatite | 0.21 |
| Troilite | 6.43 |
| Nickel Iron (Ni/Fe 1/6.3) | 7.35 |

Molecular ratio MgO/FeO in Silicate Fraction 3.14

A second analysis by the Government Chemical Laboratories, Perth, shows no significant divergence.

### X-Ray Diffraction Studies

The following minerals were recognised in the course of X-ray diffraction studies carried out at the Physics Department, University of Western Australia.

*Metallic Fraction*

Kamacite

The sulphide could not be conclusively identified.

*Silicate Fraction*

Olivine ("forsterite")

Enstatite (60% certain identification)

Rankinite (only very doubtful identification since no calcium silicate has ever been recognised in meteorites).

The recognition of orthopyroxene of the enstatite-hypersthene series was confirmed by further X-ray diffraction studies of pyroxene separated from the meteorite by Mineralogists of the British Museum (Natural History).

In the course of his investigation of olivines from stony meteorites Dr. B. Mason has carried out optical and X-ray diffraction studies of olivine from this meteorite, and confirms that it is $Fo_{75}$ $Fa_{25}$ (written communication).

### Acknowledgments

The fact that this occurrence has been recorded at all is entirely due to the interest shown by Messrs. F. R. Wickman, W. Hamlet, and C. Monger of Woolgorong Station. Dr. G. F. Claringbull and Dr. A. A. Moss of the British Museum (Natural History) assisted the writers by carrying out chemical analysis and an additional X-ray diffraction study, and Mr. J. H. Lord, Director of the Geological Survey of Western Australia, Dr. W. D. L. Ride and Mr. D. Merrilees of the Western Australian Museum contributed towards the interpretation and description of this fall. Mr. K. Bauer produced the photographic illustrations (except Plate 1 E), and Miss R. Hunt drafted the line illustrations.

### Appendix

List of institutions holding specimens of the Woolgorong Meteorite—

West Australian Museum (12113a, b and C, and thin sections 12283-12286)*.

University of Western Australia (48334).

Geological Survey, Western Australia (1/4878).

Government Chemical Laboratory, Perth (N DC 3205).

Kalgoorlie School of Mines.

British Museum (Natural History).

American Museum of Natural History, New York.

Smithsonian Institute, Washington.

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* The photomicrographs used as illustrations 3a-3f, and 4a-4b were prepared from these thin sections.

# 7.—The Agamid Lizards of the Genus Tympanocryptis in Western Australia

By G. M. Storr*

*Manuscript received—17th March, 1964*

Seven species and subspecies inhabiting Western Australia (including *parviceps* sp. nov.) are described and their distribution outlined. The relationships between *centralis*, *tetraporophora* and *lineata* are discussed. Doubt is raised whether the genus is natural. The key includes all known species and subspecies of *Tympanocryptis*.

## Introduction

The genus *Tympanocryptis*, like *Nephrurus* (Storr 1963), is most diversified in the more arid parts of Australia; and being equally difficult to collect, the discovery of its various species has been similarly protracted. Three species were described in the second half of the nineteenth century, but no more were added until Mitchell (1948) revised the genus and proposed several new taxa. The purpose of this paper is to describe yet another species, to amend the current concept of certain taxa, and to bring up to date our knowledge of the variation and distribution of all Western Australian members of the genus.

In the descriptions of species and subspecies diagnostic characters have been printed in bold-face type. Unless stated to the contrary, all material examined is lodged in the Western Australian Museum, and all localities are in this State. Since two species (*tetraporophora* and *uniformis*) are herein recorded from Western Australia for the first time, it is quite possible that other eastern taxa will be found here; accordingly *maculosa*, *intima*, and *pinguicolla* (all of Mitchell 1948) have been included in the key.

## Genus **Tympanocryptis** Peters

Type (by monotypy): *T. lineata* Peters, 1864, Mber. Akad. Wiss. Berlin **1863**: 230.

Diagnosis. Distinguishable from all other Australian Agamidae by the absence of an external ear opening.

Description. Small, terrestrial, cryptozoic and somewhat sluggish lizards with a greatly or moderately depressed head, body, and tail. The limbs, head, and tail are relatively small. The dorsal scales are heterogeneous, consisting mostly of small, smooth or keeled scales, mixed with tubercles, i.e., large scales, more or less raised and usually keeled, spinose, or mucronate. A gular fold always and a dorso-lateral fold sometimes present. Most species lack femoral pores. Pre-anal pores usually two but absent from females of most taxa.

Distribution. Endemic to Australia, where it is absent only from the east coast and south-west corner of the continent. There are seven known species, five of them occurring in Western Australia with a joint range from the Kimberley Division south to the northern Wheat-Belt, the Eastern Goldfields, and the Great Australian Bight.

## Key to Species and Subspecies

1. Dorsal tubercles conspicuous, more or less raised, with or without keels, spinose or mucronate .... 2
   Dorsal tubercles inconspicuous, flat and smooth .... *maculosa*
2. Rows of scales between nasal and labials, 4-8 .... 3
   Rows of scales between nasal and labials, 2-3 .... *parviceps*
3. Dorsal tubercles clumped in transverse and oblique ridges .... 4
   Dorsal tubercles isolated .... 5
4. Tail bands sharply oblique, usually narrower than pale interspaces .... *cephala gigas*
   Tail bands almost transverse, much wider than pale interspaces .... *cephala cephala*
5. Conspicuous dorsal pattern; neck almost as wide as or wider than head .... 6
   Moderate or obscure pattern; neck much narrower than head .... 7
6. Neck slightly narrower than head; South and Western Australia .... *lineata lineata*
   Neck slightly wider than head; southern Victoria .... *lineata pinguicolla*
7. Dorsal tubercles irregularly distributed .... 8
   Tubercles tend to be in four longitudinal rows .... *intima*
8. Hind-leg about as long as trunk .... *tetraporophora*
   Hind-leg considerably shorter than trunk .... 9
9. Eye almost completely hidden from above by bowed-out supraciliary ridge .... *lineata centralis*
   Eye protrudes from below straight supraciliary ridge .... *uniformis*

### **Tympanocryptis lineata lineata** Peters

*Tympanocryptis lineata* Peters, 1864, *supra cit.* Near Adelaide, South Australia.

Material examined. R 14184 (10 miles NE of Fraser Range HS.), R 17418 (12 miles SW of Balladonia), R 12222 (12 miles W of Naretha), R 19101-4 (Naretha), R19105-10 (Seemore Downs), R 15209 (Rawlinna), R 16502 (Forrest).

Description. Moderately stout and depressed. **Sides of neck puffed out almost to width of head.** Supraciliary ridge moderately acute and (viewed from above) only slightly bowed outwards and not concealing the somewhat protrusive eyes. Facial trough not deep or angular. Snout-vent length of largest specimen (R 19103, a gravid ♀) 65 mm.

Rostral 2-3 times as wide as first labial. Mental truncate polygonal or elliptical, deeper than wide, and usually narrower than rostral. Upper labials 12-15. Nasal approximately heptagonal, flat or slightly convex, the moderately large oval nostril piercing it towards the top and entering forwards and downwards, and separated from the labials by 4-5 rows of tectiform scales.

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* Western Australian Museum, Perth, Western Australia.

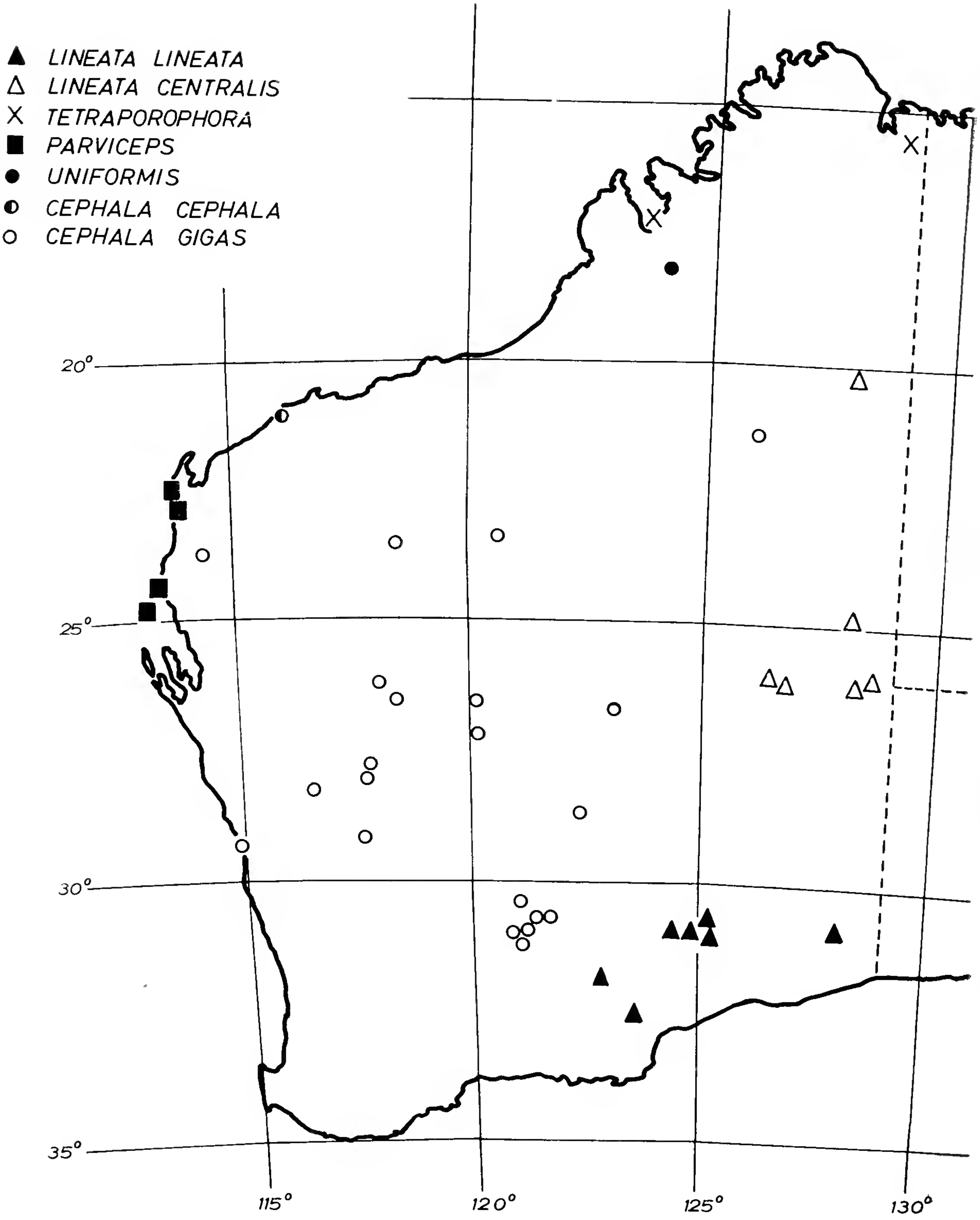

Fig. 1.—Map of Western Australia, showing location of specimens of *Tympanocryptis*.

Scales on top of head strongly keeled, usually unicarinate but occasionally multicarinate or rugose, smallest above the temples and supraciliary ridge. Scales on nape small and bluntly keeled, becoming larger and more strongly keeled on back, where they are mixed with scattered tubercles, i.e. scales that are enlarged, raised, sharply keeled and mucronate. Tubercles are absent from the longitudinal white lines and tend to be sparse in the space between the dark transverse bands. There are some tubercles on the base of the tail, but distally the scales are more uniform, their keels aligned longitudinally. Scales on upper surface of limbs (like tail) large and strongly keeled; on the under surface smaller and feebly keeled.

Gulars and ventrals smooth. Palms and soles covered with small, imbricate, bluntly keeled scales. Lamellae under fourth toe 18-22, spinose and sharply bicarinate. Claws relatively short. Pores in both sexes, 2 pre-anal and occasionally a small one on thigh.

Dorsal ground colour fawn. Five prominent silvery grey or white longitudinal lines running back from neck; of these the vertebral is much the widest (4 times as wide as the dorsolaterals) and, like the laterals, ends at the level of the pelvis; the dorso-laterals reach the proximal third of tail. These lines dilate as they cross over dark chocolate-brown bands (a broad one across neck, 4 narrower ones across body, and 12-17 indistinct ones on tail) and may become brownish where they cross the pale interspaces. The transverse bands are widest where they contact the vertebral line. The squares bounded by the transverse bands and the vertebral and dorso-lateral lines are somewhat paler and less reddish than the corresponding spaces between the dorso-lateral and lateral lines. Upper surface of limbs, like tail, vaguely banded with chocolate-brown. A short dark chocolate transverse bar in front and a short longitudinal bar to each side of interparietal. A pale transverse bar from orbit to orbit, with an ill-defined dark bar immediately in front of it. Under surface whitish except for grey or black flecking on chin, chest or abdomen (these dark scales, especially on chin, may be arranged in broken, more or less longitudinal lines).

Distribution. South-eastern Western Australia west to Fraser Range and east through southern South Australia to north-western Victoria where it begins to intergrade with the south Victorian race *pinguicolla* (Mitchell 1948).

### **Tympanocryptis lineata centralis** Sternfeld

*Tympanocryptis lineata centralis* Sternfeld, 1924, Abh. Senckb. Naturf. Ges. 38: 234. Hermannsburg Northern Territory (M. von Leonhardi).

Material examined. R 21861-4 (Balgo Hills Mission), R 15141-3 (Warburton Range Mission), R 15696 (20 miles E of Warburton Range Mission), R 20988 (western pass, Blackstone Range), R 20746 (Blackstone Mining Camp), R 20757-8 (Pass of the Abencerrages, Rawlinson Range), R 21454-6 (Tennant Creek, Northern Territory), R 20925 (Victory Downs, Northern Territory).

Description. More slender than nominate race, with **narrower neck and shorter tail and limbs.** When viewed from above, supraciliary ridge more strongly bowed outwards and concealing more but not all of eye. Snout-vent length of largest specimen (R 21456, a gravid ♀) 61 mm.

Rostral less than twice as wide as first labial. Mental usually deeper than wide and narrower than rostral. Upper labials 10-14.

Head scales more uniform in size and less strongly keeled than in nominate race, especially in vicinity of interparietal where they may be quite smooth. Supratemporals not markedly smaller than neighbouring scales. Dorsals more heterogeneous than in nominate race, with a greater contrast between the smooth or slightly keeled, weakly imbricate small scales and the sharply keeled, spinose tubercles.

**Gulars and ventrals weakly keeled.** Lamellae under fourth toe 15-21, mostly unicarinate, becoming bicarinate distally. Claws, especially those of fingers, much longer than in nominate race, and the longest in the genus. Two preanal and occasionally a small femoral pore (pores are seldom discernible in females).

Coloration darker (reddish or purplish brown) and **less strongly patterned** than in nominate race. The longitudinal lines, especially the laterals, may be obscure or absent. When present, the vertebral line is only twice (not four times) as wide as the dorsolaterals.

Distribution. Hills of the far eastern interior of Western Australia, east into the Northern Territory and probably north-western South Australia (R 20925 was taken about a mile north of the South Australian border).

Comments. Loveridge (1934) wrote, "the grounds on which Sternfeld based this race are somewhat slender". They certainly were, for one of his two characters was invalid, *viz.* that *centralis* has a much longer tail than typical *lineata*. Sternfeld had no specimens of the latter and relied on the imperfect description in Boulenger (1885). Mitchell (1948) went so far as to relegate *centralis* to the synonomy of *lineata lineata*. Yet *centralis*, as the foregoing description shows, differs consistently and markedly from *lineata*, which occurs only 300 miles to the south and is quite uniform throughout its extensive range in the south-east of this State and, judging from Mitchell's photographs and descriptions, in southern South Australia.

I have hesitated to include in *centralis* a specimen (R 13222) from Giles. More material is required before deciding whether the discrepancies between it and *centralis* are due to its youth (snout-vent length 25 mm.) or are characteristic of another but undescribed taxon. There is no indication of longitudinal white lines; and the dorsal tubercles are large, obtusely keeled, not spinose or even mucronate, and tend to be aligned longitudinally. It is thus similar in some respects to the two specimens from the northern MacDonnell Ranges, described briefly by Mitchell (1948, p. 70).

### **Tympanocryptis tetraporophora** Lucas & Frost

*Tympanocryptis tetraporophora* Lucas & Frost, 1895, Proc. Roy. Soc. Vic. 7: 265. Adminga, South Australia (W. Baldwin Spencer).

Material examined. R 11752 (Kimberley Research Station, Ord River), Macleay Mus. R 930 (King Sound), National Mus. D 7701 (holotype), Description. **Relatively slender with a narrow head and long legs.** Tail long, tapering gradually. **Supraciliary ridge** acute and (viewed from above) fairly **straight** in outline and **almost wholly concealing eye.** Rostral ridge acute. Facial trough shallow and rounded (R 930) or deep and angular (R 11752). Snout-vent length of largest specimen (R 930, a presumed ♀), 63.5 mm.

Rostral 3-4 times as wide as high, wider than polygonal mental, about equal to combined width of first two labials. Nasal situated on or below rostral ridge, elliptical or rounded polygonal, convex, pierced a little above its centre by the large elliptical nostril which enters forward, and separated from labials by 4-5 rows of facials. Upper labials 11-15, increasing in size backwards, tectiform or keeled, and as large as or larger than adjacent facials.

Scales on top of head mostly with a strong keel, sometimes tricarinate or rugose, smallest above orbits, and largest on occiput and temples. Scales on nape small, strongly imbricate, keeled or spinose, becoming larger on back where they are irregularly mixed with tubercles, i.e. larger, raised scales which are strongly keeled and spinose. Extreme base of tail has scattered tubercles, not much larger than the sharply keeled, mucronate ordinary scales. Scales on upper surface of limbs large, sharply keeled, and mucronate or spinose.

Scales on chin keeled, becoming larger, mucronate and more strongly imbricate on throat. Ventrals large, imbricate, keeled and mucronate. Subcaudals similar in size to supracaudals but less strongly keeled, not spinose and only slightly mucronate, the keels aligned longitudinally. Scales on palms and soles strongly imbricate, raised, and trispinose (the central spine much the highest). Lamellae under fourth toe 19-21, bicarinate and trispinose (the outer spine much the smallest and not arising from a keel). Claws moderately long. Pores in males only, 2 pre-anal.

Head and back brownish grey, becoming paler on distal half of tail. Indistinct brown bands across back, narrowly broken by the vertebral and dorso-lateral lines which, being little paler than the ground colour, are scarcely discernible. Several caudal bands, of which the first 2-4 are darkest and least obscure. Limbs paler than back, not or vaguely banded. Under surface whitish, with or without brown flecking.

The above description is based on the two Kimberley specimens, which differ as much among themselves as from the type, which I have been able to examine through the courtesy of Mr. J. McNally, Director of the National Museum, Melbourne. The rostral is higher in the type, so that it is only twice as wide as high and no wider than the mental. The obtuse rostral ridge is swollen around the nasal, which is separated from the labials by 6-7 rows of facials. Most of the head scales in the type have one or more small pits near their posterior edge.

Distribution. Restricted in Western Australia to the Kimberley Division. (Owing to past confusion of this species with *lineata*, it is not possible to ascertain from the literature its distribution beyond this State. It probably extends from the Kimberleys south and east through the Northern Territory to far northern South Australia.)

Comments. Lucas and Frost founded this species mainly on its possession of femoral pores. A year later (1896) they virtually retracted it after discovering, as I have done, that *lineata* too may have femoral pores. Nevertheless, *tetraporophora* is a recognisable taxon, differing from *lineata* in having little colour pattern, a more slender habitus, and considerably longer limbs. The only question is whether it or *centralis* represents *lineata* in central Australia. Only one of them can be regarded as a race of *lineata*, for they are almost certainly sympatric over a large part of the Northern Territory (they may however be ecologically separated, for *centralis* has only been found among rocks). I have retained *centralis* as a race of *lineata*, because of its greater similarity in colouring. It is interesting that *centralis* and *tetraporophora* diverge from *lineata* in opposite directions with respect to length of limbs.

### Tympanocryptis parviceps sp. nov.

Holotype. R 16984 (in Western Australian Museum), an adult ♂ collected by G. M. Storr and B. T. Clay on October 18, 1962.

Type Locality. Eleven miles south-east of Ningaloo, Western Australia, in 22° 48′ S, 113° 49′ E.

Paratypes. R 19095-6 (2 miles N of Ningaloo); R 8833, R 13221, R 13483, R 19094 (Point Cloates); R 19097-8 (Quobba); R 10654, R 11265-70, R 13164, R 20494-5 (Bernier Island).

Description. Body relatively slender, moderately depressed. Head small, not greatly wider than neck. Fore-legs short, hind-legs long. Supraciliary ridge acute and (viewed from above) bowed outward and concealing most of eye. Rostral ridge continuous with supraciliary ridge and similarly acute. Facial trough deep and angular. **Chin terraced,** i.e. the plane of the chin, instead of curving gradually round the ventro-lateral corner of jaw changes abruptly along a straight line running obliquely back from each side of mental (see Figure 2). A small but distinct **dorso-lateral fold.** Snout-vent length of largest specimen (R 19094, a ♀) 46.5 mm.

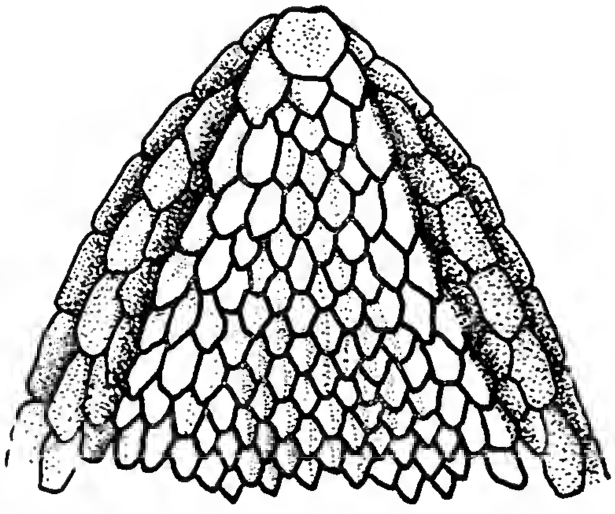

Fig. 2.—Ventral surface of head of *T. parviceps* illustrating the "terracing" of chin. Drawn by Miss R. Hunt.

Rostral much wider than high, about equal to combined width of first two labials, and wider than the hexagonal or truncate polygonal or elliptical mental, which is nearly as wide as deep. Upper labials 8-12, keeled, much smaller than the facials immediately above them. **Nasal** large, situated well below rostral ridge and **extending to bottom of facial trough**, rounded polygonal, flat or slightly concave, pierced towards its top by an elliptical nostril which enters downwards and forwards, and **separated from labials by 2 (sometimes 3) rows of facials**, the upper row small and smooth, the lower large and keeled.

Scales on top of head strongly keeled, largest in the frontal and interpariental regions, smallest above the supraciliary ridge and on the occiput where they become rugosely conical. Scales on nape small but strongly keeled. Scales in wide strip down middle of back uniform, slightly raised, strongly keeled and weakly spinose. Dorso-laterals vary greatly in size, the smallest being little larger than the nuchals. Caudals similar to but larger than median dorsals. Scales on upper surface of limbs similar to median dorsals.

Scales on chin weakly keeled, becoming higher and subspinose on throat. Ventrals large and mucronate on chest, becoming smaller and weaker on abdomen. Scales on under surface of limbs similar to those on chest. Scales on palms and soles flat and weakly keeled. Lamellae under fourth toe 18-23, bicarinate and bispinose (the outer spines much the smaller). Claws slender and moderately short. Pores in ♂♂ only, 26-34 (8-10 pre-anal, 16-25 femoral).

Dorsal ground colour pale brownish grey, palest and tending to fawn on the median dorsal strip (where all the scales are uniformly large). The dark brown on sides of body and tail extends on to dorsum in the form of narrow hourglass-shaped bars, broken by the pale median strip. Limbs not or vaguely banded with brown. Under surface whitish except for grey or black marbling on chin and throat.

Distribution. Mid-west coast of Western Australia from Ningaloo south to Quobba and Bernier Island.

Comments. This is the most distinctive species in the genus, and its belated description has been due to its confusion with *Amphibolurus adelaidensis* rather than to its restricted distribution. Within its range it is apparently plentiful, especially at Point Cloates where several specialists in other animal groups have incidentally collected *parviceps*.

Lacking an external ear opening and a lateral line of tubercles on the base of tail, *parviceps* should never have been mistaken for *adelaidensis*. Nevertheless their similarity is more than superficial; for these two species, alone among the Agamidae I have examined, possess a "terraced" chin. In view of this and of similarities in colour pattern and dorsal scalation, they are believed to be more closely related to each other than to any species in the genus to which they are at present assigned.

### **Tympanocryptis uniformis** Mitchell

*Tympanocryptis uniformis* Mitchell 1948, Rec. S. Aust. Mus. 9: 76. Near Darwin, Northern Territory (P. Wesselmann).

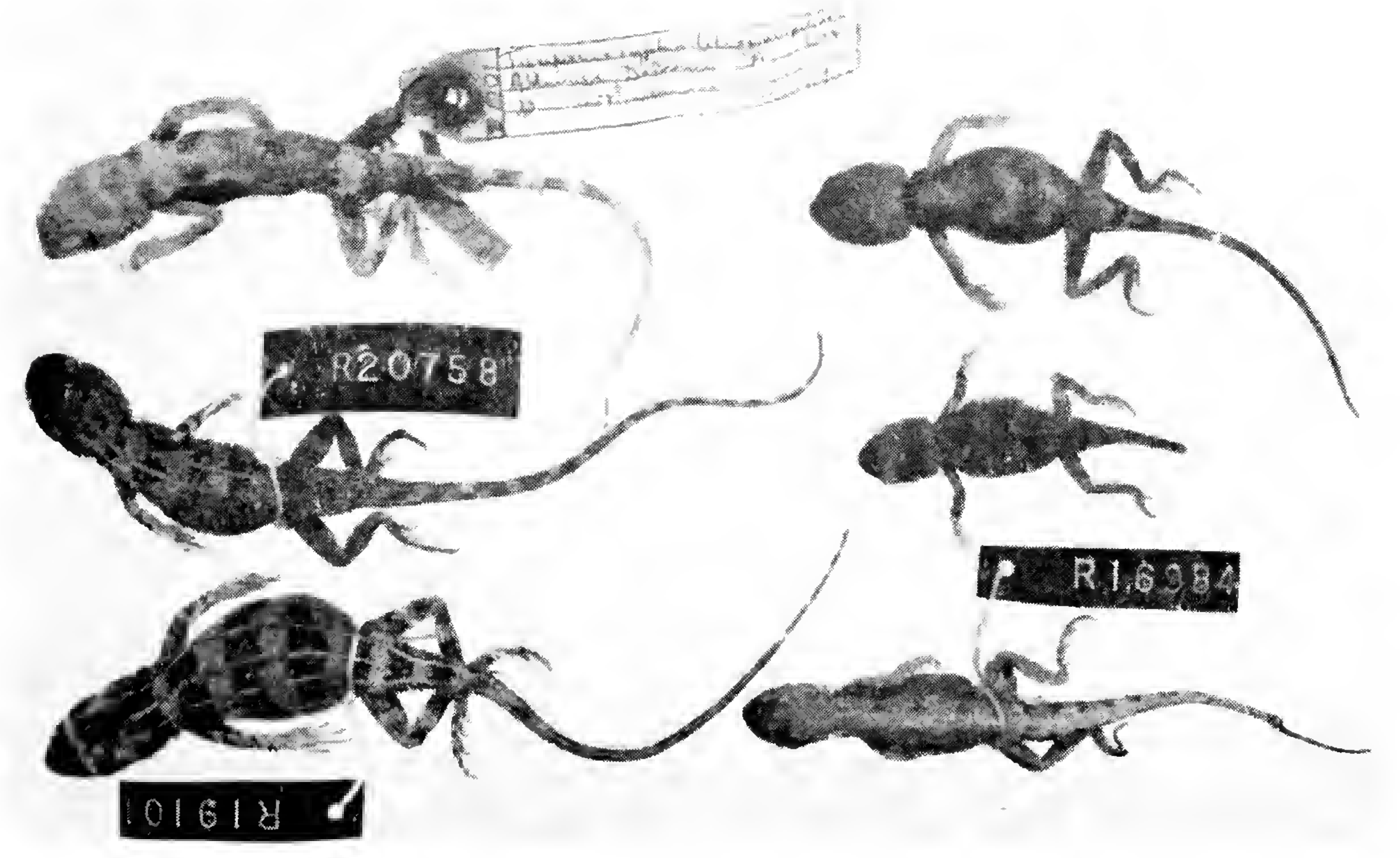

Fig. 3.—Left (top to bottom): *Tympanocryptis tetraporophora, T. l. centralis,* and *T. l. lineata.* Right (top to bottom): *T. cephala gigas, T. uniformis,* and *T. parviceps.*

Material examined. R 13638 (20 miles SE of Luluigui, West Kimberley).

Description. Body moderately depressed. Head large. **Snout short, sloping steeply in profile.** Limbs small. **Tail tapering rapidly** (as in *T. cephala*). Supraciliary ridge acute and (viewed from above) straight in outline and not concealing the **very protrusive eyes.** Rostral ridge obtuse. Facial trough shallow but angular.

Rostral a little more than twice as wide as high, slightly wider than combined width of first two labials, and a little wider than the truncate elliptical mental. Upper labials 15, increasing in size backwards, and considerably smaller than the facials immediately above them. Nasal situated on swollen rostral ridge, rounded polygonal, convex, pierced towards its top by a small circular nostril which enters downwards and forwards, and separated from labials by 5-6 rows of facials.

Scales on top of head strongly keeled anteriorly, becoming rugose posteriorly, smallest above supraciliary ridge, largest prefrontally and around interparietal. Dorsals weakly imbricate, weakly keeled, mucronate, and sparsely mixed with isolated tubercles (enlarged, slightly raised, unicarinate scales, their keel terminating in a short spine or mucro), which are highest on sacrum. The largest tubercles tend to be aligned in four longitudinal rows, two on each side of dark vertebral stripe, which consists of two rows of uniform black scales, slightly larger and more strongly imbricate and keeled than other dorsals. Tubercles extend to base of tail, which is otherwise covered above with keeled mucronate scales, and below with non-imbricate scales whose keels are aligned more regularly. Scales on upper surface of limbs more strongly keeled. Two highly spinose scales towards posterior edge of thigh.

Scales under head mostly smooth and weakly imbricate. Ventrals largest on chest and tending to be striate or weakly keeled. Scales on lower surface of limbs much smaller and less strongly keeled than those above. Scales on palms and soles still smaller but more sharply keeled, distally becoming spinose, especially on palm. Lamellae under fourth toe 16-18, strongly bispinose, except proximally where the outer spines are scarcely discernible. Claws short and stout. No pores.

Dorsal ground colour grey. Body and tail crossed by darker grey bands (of uniform width and as wide as interspaces), one across neck and four across body, all of them only slightly darker than ground coloration and thus barely discernible. Caudal bands darker and more prominent, at least on proximal half of tail. More conspicuous than the body bands is a dark grey or black vertebral strip from occiput to rump. Much fainter are a dark discontinuous dorso-lateral and lateral line, discernible only where they cross the transverse bands. Limbs pale greyish brown, obscurely banded with darker brown. Entire under surface white except for pale greyish brown flecking round jaws.

Distribution. From the Kimberley Division of Western Australia east into the Northern Territory.

Comments. The above description is of specimen R 13638, collected by Prof. C. L. Camp on June 23, 1960, which constitutes the first record for this State and the only known specimen apart from the type.

### Tympanocryptis cephala gigas Mitchell

*Tympanocryptis cephalus gigas* Mitchell, 1948, Rec. S. Aust. Mus. 9: 65. Between Ashburton and Gascoyne Rivers, Western Australia.

Material examined. R 3990 (between Wells 40 and 43, Canning Stock Route); R 13363 (Jigalong); R 13640, R 17689 (Turee Creek); R 14060 (Wandagee); R 19111 ("Bernier Island"); R 13476 (20 miles S of Dongara); R 19099 (11 miles N of Mt. Magnet); R 13639 (Yalgoo); R 13991 (Paynes Find); R 19649 (Mt. Magnet); R 15802 (Belele); R 2006 (Meekatharra); R 7302 (Wiluna); R 1606 (Lake Wells); R 19770 (Albion Downs); R 1240, R 1242, R 1305, R 1360, R 1757-8, R 13323 (Laverton); R 20-1 ("Goldfields"); R 7067 (Grants Patch); R 3748 (Hampton Hill); R 4329, R 6542-4 (Kalgoorlie); R 6434-5, R 6754-5 (Kurrawang); R 2346 (Londonderry); R 19100 (10 miles W of Coolgardie).

Description. **Body much depressed. Neck much narrower than head, which is usually a little wider than long. Tail short, tapering rapidly.** Supraciliary ridge moderately acute and (viewed from above) bowed out but not concealing eye. Rostral ridge obtuse, swollen in front of nasal. Facial trough not deep or angular. Snout-vent length of largest specimen (R 6755) 57 mm.

Rostral about twice as wide as high, slightly narrower than combined width of first two labials, and considerably wider than the truncate elliptical mental which is usually deeper than wide. Upper labials 12-16, smaller than the facials immediately above them. Nasal situated immediately below rostral ridge, rounded polygonal, slightly convex, pierced a little above its centre by the small elliptical nostril which enters downwards and slightly forwards, and separated from labials by 5-6 rows of facials.

Scales on top of head rugosely tectiform or conical; largest and highest prefrontally, on temples, and around interparietal; smallest and lowest above supraciliary ridge and on mid-line between orbits. Scales on nape small and strongly imbricate, becoming larger and weakly imbricate or juxtaposed on back. **Dorsal tubercles** large, raised, **unkeeled,** trispinose (the central spine much the highest and sharpest) and **arranged side by side to form short transverse or oblique ridges;** the two kinds of tubercular ridge generally alternate down the back, the transverse ridges tending to be distant from the mid-line, and the oblique ridges close to it. The tubercles extend to base of tail, the remainder of its upper surface, like its entire under surface, being covered with uniform scales, their keels aligned longitudinally.

Scales on chin imbricate and weakly keeled. Ventrals weakly imbricate and keeled on chest, becoming smooth and juxtaposed on abdomen. Except at elbow and knee, scales on upper surface of limbs large, strongly keeled and mucronate, and mixed on fore-arm and thigh with tubercles like those on back. Scales on lower surface of limbs similar to subcaudals. Scales on palms and soles small, strongly keeled, and spinose. Lamellae under fourth toe 16-18, bicarinate and bispinose, the outer keels and spines much the smaller and sometimes barely discernible. Claws strong and short. Two preanal pores in most specimens.

Dorsal ground colour brownish red. **A dark reddish brown band across narrowest part of neck,** sometimes broken by 3 short white longitudinal lines (one vertebral, two dorso-lateral). 8-11 dark bands across tail. The first caudal band, situated only a little behind level of vent, is transverse and has a sharply defined darker posterior edge. The next two bands are increasingly oblique (from above they appear V-shaped with the angle pointing backwards), similarly with a dark posterior edge, and separated from each other (as are the first and second bands) by a large whitish or pale grey space. The remaining caudal bands are more obscure and uniform in colour (i.e. not darkly margined) and tend to be broken and to extend to lower surface of tail. Limbs vaguely banded. Entire under surface whitish.

Distribution. Western Australia, from the Ashburton River drainage and the Great Sandy Desert south to Dongara, Paynes Find, and the vicinity of Kalgoorlie.

Comments. The above description is based on specimens from the Eastern Goldfields, the only region from which there is adequate material. Northwards, the following changes occur:

(1) the head scales become lower and less rugose and tend to be simply unicarinate or smooth;

(2) the head becomes narrower than long;

(3) the tubercles become smaller, lower, less numerous and not so inclined to be arranged in definite and symmetrical patterns;

(4) the nasal tends to move up on to rostral ridge.

North to at least the Ashburton, there is no geographical variation in colouring, apart from a tendency for the flanks to become dark grey, which may diffuse on to back broadly or in the form of vaguely transverse bands. The head may be similarly diffused with grey above orbits and temples.

Though the extreme populations are fairly distinct, they are connected by a chain of intermediates. Moreover, the various north-south clines seem to operate independently of each other and any division into two races would necessarily be arbitrary. Mitchell's concept of *gigas* is therefore broadened so as to include all populations south of the Ashburton.

### **Tympanocryptis cephala cephala** Günther

*Tympanocryptis cephalus* Günther 1867, Ann. Mag. Nat. Hist. (3) **20**; 52. Nickol Bay, Western Australia (Duboulay).

Material examined. R 12495 (Mardie).

Distribution. A small sector of the north-west coast of Western Australia, west of Roebourne.

Comments. As nominate *cephala* is only known from the two syntypes in the British Museum and from our R 12495, it is not possible to give a full description of it. All that can be done at present is to show briefly how *cephala* differs from the much better known *gigas*.

According to the original description, Boulenger (1885), and the photograph of a syntype (Mitchell 1948), nominate *cephala* differs from *gigas* as follows:

(1) the body is not so depressed, and the head is narrower

(2) the dorsal tubercles are not (or not so markedly) arranged into welts

(3) there are darker bands ("more or less indistinct") across the body

(4) the caudal bands are separated from each other by much narrower interspaces.

The specimen from Mardie (only 60 miles south-west of the type locality) is very young (snout-vent length 26.5 mm) but seems essentially similar to the syntypes. It further differs from our series of *gigas* in having

(1) more strongly keeled and imbricate ventrals (this is especially noticeable on the abdomen, where the scales show no tendency to become smooth and juxtaposed)

(2) fewer lamellae (13) under the fourth toe, compared with 14-19, seldom fewer than 16, in *gigas*

(3) much weaker spines on palms, soles and subdigital lamellae (indeed the last 2-3 lamellae are quite smooth).

In some characters, e.g., the relative smoothness of head scales and the position of the nostril with respect to the rostral ridge, typical *cephala* is nearer to northern *gigas* than the latter is to southern *gigas*. In other characters, especially coloration, there is sharp enough break to warrant at least tentatively the recognition of the two races.

#### **Measurements**

The following measurements were made on all specimens: (1) total length, (2) length of tail, (3) snout-vent length, (4) length of hind-leg (including longest toe, without claw)—all to the nearest 0.5 mm; and (5) length of head (measured axially from snout to end of lower jaw) and (6) maximum width of head—both to nearest 0.1 mm. All these measurements were expressed as per cent. length of trunk (snout-vent length minus length of head), and the mean and standard deviation from the mean were calculated for each sample; with the exception of head width they are given in Table I. For the number of specimens examined in each taxon

**TABLE I**

*Mean length of head, tail, fore-leg, and hind-leg, all expressed as per cent. length of trunk (with standard deviation in brackets).*

| | Head | Tail | Fore-leg | Hind leg |
|---|---|---|---|---|
| *l. lineata* .. | 40·2(4·2) | 226·1(22·4) | 59·3(4·5) | 93·5(9·1) |
| *l. centralis* . | 37·7(2·4) | 205·5(19·3) | 55·8(3·4) | 82·1(5·2) |
| *tetraporophora* | 37·5 | 216 | 63·3 | 101·7 |
| *parviceps* .. | 36·2(2·8) | 196·2(21·6) | 54·0(4·8) | 99·4(7·5) |
| *uniformis* . | 42 | | 58 | 85 |
| *c. cephala* ... | 43 | 141 | 60 | 92 |
| *c. gigas* .... | 40·6(4·6) | 175·6(18·9) | 65·7(4·8) | 92·3(6·9) |

**TABLE II**

*Number of specimens examined, mean length of trunk, ratio fore-leg to hind-leg, and ratio width to length of head (with standard deviation in brackets).*

| | Number of Specimens | Length of Trunk (mm) | Fore-leg as % of Hind-leg | Width of Head as % of its Length |
|---|---|---|---|---|
| *l. lineata* .... | 15 | 36·4 | 63·6(3·3) | 83·4(4·6) |
| *l. centralis* ... | 18 | 34·9 | 67·1(2·7) | 87·6(3·4) |
| *tetraporophora* | 3 | 42·0 | 62·0 | 82·0 |
| *parviceps* .. | 19 | 28·8 | 54·3(3·9) | 87·0(2·5) |
| *uniformis* | 1 | 24 | 68 | 91 |
| *c. cephala* ... | 1 | 18·5 | 65 | 100 |
| *c. gigas* | 36 | 29·3 | 70·6(3·3) | 99·6(5·8) |

see Table II, which also gives mean length of trunk and mean ratio length of fore-leg to hind-leg and width to length of head.

Tables I and II show that the *lineata* group (including *tetraporophora*) comprises larger and longer-tailed lizards than in the rest of the genus.

Despite its broken distribution (in isolated ranges surrounded by sandy deserts or otherwise unsuitable lowlands), *lineata centralis* exhibits remarkably little variability in the relative length of its appendages. In contrast, the more continuously distributed *lineata lineata* is highly variable in structure (probably exceeding in this respect *cephala gigas*, which undergoes marked clinal variation in several characters). However, *l. lineata* is much more uniform in coloration than *l. centralis*, which tends to lose its dorsal pattern from east to west.

## Discussion

As illustrated by the map in Mitchell (1948, p. 58), the genus *Tympanocryptis* attains its greatest diversity in the Lake Eyre basin. In Western Australia, however, the several taxa tend even more than in *Nephrurus* (Storr 1963) to be allopatric. There is probably widespread sympatry only in the Kimberley Division (between *uniformis* and *tetraporophora*). Further collecting in the far east of the State may reveal the presence of *tetraporophora* within the range of *lineata*. Elsewhere the probability of sympatry is small. As *parviceps* is restricted to coastal dunes, it will at most only approach the range of *cephala*, which alone represents the genus on the great Precambrian block from the Pilbara south to the Goldfields.

Since this study was begun it has become increasingly doubtful whether the genus *Tympanocryptis* is tenable as it is at present understood. As mentioned earlier, *parviceps* is in some important respects more like *Amphibolurus adelaidensis* than any *Tympanocryptis*. On the other hand, the 2-pored species of *Tympanocryptis*, especially the *lineata* group, are reminiscent of various species of *Diporiphora*.

The closure of the ear aperture has, perhaps, no great phylogenetic significance. At any rate, if *Tympanocryptis* is to stand, other characters should be found. The relatively small head cannot be reckoned an independent character, for it is almost certainly related to the atrophy of the ear, which in turn is probably connected with their small size and sedentary and cryptic habits. There thus remains at present only their tendency to spininess, which however is shared with such species of *Amphibolurus* as *adelaidensis* and *barbatus*. Indeed, the latter, with its extremely depressed body, differs from *Tympanocryptis* only in its larger size and the presence of an ear aperture.

The generic classification of Australian Agamidae has remained exactly as Boulenger left it in 1885, and a thorough and simultaneous revision of all Australian genera is long overdue. Since such a study has been planned by another worker, I have not pursued the matter further and have retained for the present *Tympanocryptis* in its traditional sense.

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# 8.—On Beryl from Western Australia

By P. L. C. Grubb*

*Manuscript received—19th November, 1963*

Varieties of pink, light blue, and white beryl are described from two localities in Western Australia. Their contrasting features are examined by optical, physical, x-ray diffraction, chemical, and spectrographic means. The slight differences in colour are considered to be caused by a variety of factors including trace element distribution, minute partially crystallised fluid inclusions, and the degree of incipient kaolinisation. The effect of alkali ion content on unit cell parameters is examined but fails to reveal any consistent relationship. Finally, the nature and composition of former liquid inclusions is briefly analysed and comparisons with other reported samples drawn.

## Introduction

Of the three varieties of beryl discussed here, two (the light blue and white) were collected from the undulating Mt. Marion pegmatite sheet (Lat. 31° 5′ S., Long. 121° 30′ E.), where they form part of a single large zoned crystal. The third (a reportedly caesium-bearing type) was obtained from a pegmatite body at Wodgina (Lat. 21° 25′ S., Long. 118° 30′ E.).

## Optical and X-Ray Diffraction Properties

*Zoning.*—Although isomorphous replacements of several elements within the beryl crystal lattice are common, macro- and microscopic zoning of single crystals appears to be quite rare. The total diameter of the zoned Mt. Marion crystal is of the order of 3 cm and the outer cloudy white zone is between 4 and 8 mm thick. The junction of these two zoned portions is quite sharp, but in one section it consists of a gradational fine-scale repetition of these.

*Refractive indices.*—Slight variations in refractive indices between the three main beryls exist (Table 1), and it is noteworthy that in the pink Wodgina beryl the incipiently kaolinised portions have refractive indices up to 0.002 higher than the fresh grains.

**TABLE 1**

Refractive indices of Western Australian beryls

| | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Ne | 1·577 | 1·576 | 1·581 | 1·576 |
| No | 1·586 | 1·588 | 1·591 | 1·583 |

1. Light blue core } Mt. Marion zoned beryl crystal
2. Cloudy white margin } Mt. Marion zoned beryl crystal
3. Pink beryl from Wodgina
4. Clear green beryl from Yinnietharra (Norrish 1950)

*Inclusions.*—In all three beryls microscopic rod-like inclusions occur, these being most conspicuous in the clear light blue and pink varieties (Fig. 1 and 2). Despite their superficial resemblance to those figured by Little (1960) however, these differ in being partially or sometimes wholly crystalline so that on fine pulverising—particularly in the Wodgina beryl—they can be isolated from larger grains and their refractive indices compared with those of immersion oils.

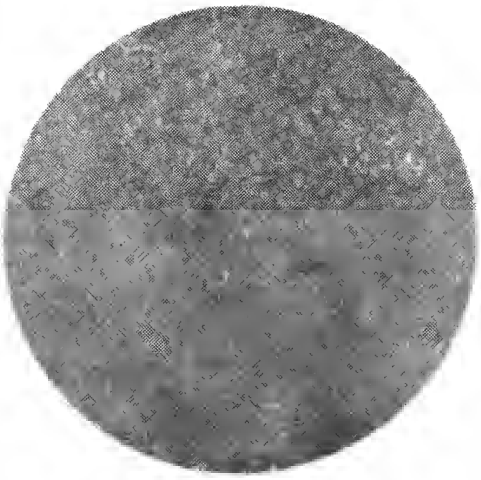

Fig. 1.—Rod-like quartz inclusions in Mt. Marion beryl. Plain polarised green light. X 250 magnifications.

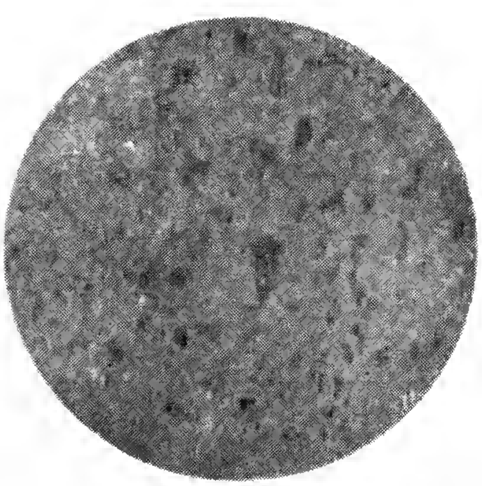

Fig. 2.—Fluorite inclusions in pink beryl from Wodgina, Western Australia. Plain polarised green light. X 480 magnifications.

Identification of these solid inclusions was carried out by x-ray diffraction with the result that traces of quartz were discerned in the light blue variety and of fluorite in that of Wodgina.

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It is also of interest to note that whereas Norrish (1950) observed minute tubular inclusions of "water" parallel to the "c" crystallographic axis in beryl from Yinnietharra, he found no evidence of this water in a complete chemical analysis of the same specimen.

*Alteration.*—Although no traces of secondary alteration products were detectable by x-ray diffraction means, close scrutiny under high magnification revealed a slight dusting effect of some grains in the cloudy white variety and to a lesser extent in the pink variety. This, as at Mt. Marion, is coupled with a slightly higher loss-on-ignition of the outer white crystal margin compared with the clear light blue core. It seems logical to conclude therefore, that the conspicuous white appearance of some beryl from Mt. Marion is caused by incipient kaolinisation.

*Unit cell parameters.*—Calculation of the unit cell parameters for the three beryl types from Mt. Marion and Wodgina show slight divergencies but this appears to bear no evident relationship to their chemical composition (Table 2). No support therefore can be found here for the hypothesis of Sosedko (1957) and Frank-Kamenetsky & Sosedko (1958) that the "c" unit cell parameter increases stoichiometrically with the alkali content due to the crystal lattice distortion caused by the substitution of small beryllium ions by larger alkali ions. Neither does there appear to be a very constant relationship between the "a" unit cell parameter and total alkali ion content as suggested by Schaller, Stevens and Jahns (1962).

*Specific gravities.*—Specific gravities determined using the Berman precision balance show the highest values for the pink Wodgina beryl, whereas the cloudy white Mt. Marion beryl, being slightly kaolinised, is less than its light blue counterpart (Table 2).

*Chemical analyses.*—Partial chemical analyses of the three beryl types from Wodgina and Mt. Marion are listed in Table 2. In addition qualitative and semi-quantitative spectrographic anaylses of each showed slightly higher contents of cobalt and manganese in the pink Wodgina sample, slightly more titanium and zinc in the blue Mt. Marion type, and rather more aluminium, magnesium, calcium, iron, chromium, sodium, and lithium in the white Mt. Marion beryl. It is of interest, however, that no caesium could be detected in any of the samples studied.

## Conclusions

Inclusions in beryl, although rare, have recently been described from several world localities, yet for the most part these are believed to be fluid bodies consisting essentially of water, carbon dioxide, and sulphur (Little 1960 and Zwaan 1958). Eppler (1958), on the other hand, considers that the chatoyancy exhibited in some beryl crystals is due to minute oriented ilmenite needles. Subsequently (1960) in an almost opaque beryl sample showing asterism, he recorded thin tabular pyrrhotite crystals, crystal groups of quartz and epidote, rod-like apatite, and clusters of pyrite. Most recently Schaller, Stevens, and Jahns (1962) have recorded oriented inclusions of quartz, tourmaline and fluorite in an unusual beryl from Arizona.

The inclusions in both the Mt. Marion and Wodgina beryls, although now largely crystalline, appear to have consisted of the late residual fluid existing while the beryl was in the

**TABLE 2**

Chemical composition and calculated unit cell constants for beryl

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| $SiO_2$ | | | | 64·85 | 65·32 | 64·17 | 61·88 |
| $BeO$ | | | | 13·15 | 12·60 | 11·82 | 10·54 |
| $Al_2O_3$ | | | | 17·52 | 17·77 | 17·42 | 17·10 |
| $Fe_2O_3$ | | | | 0·37 | 0·13 | 0·12 | 0·08 |
| $MgO$ | | | | 0·14 | 0·25 | 0·21 | 0·22 |
| $CaO$ | trace | trace | 0·07 | nil | 0·26 | 0·44 | 0·44 |
| $Li_2O$ | 0·34 | 0·60 | 0·64 | 0·52 | 0·30 | 1·23 | 0·60 |
| $MnO$ | ... | | | 0·01 | trace | nil | trace |
| $Na_2O$ | 0·64 | 1·66 | 1·00 | 0·94 | 1·27 | 1·39 | 2·50 |
| $K_2O$ | 0·46 | 0·16 | 0·16 | 0·46 | nil | nil | nil |
| $(Rb\ Cs)_2O$ | nil | nil | nil | 0·08 | 0·27 | 0·67 | 4·13 |
| $H_2O+105°C$ | 2·10 | 2·55 | 1·84 | 2·19 | 1·76 | 1·88 | 2·26 |
| $H_2O-105°C$ | 0·70 | 0·00 | 0·00 | nil | 0·08 | 0·60 | 0·16 |
| $TiO_2$ | trace | trace | ... | nil | 0·01 | 0·01 | 0·01 |
| $P_2O_5$ | | | ... | nil | ... | .... | .... |
| $Cr_2O_3$ | trace | trace | .... | nil | ... | ... | .... |
| $F$ | | .... | | nil | .... | ... | .... |
| $Cl$ | | ... | | nil | ... | ... | |
| | | | | 99·93 | 100·02 | 99·96 | 99·92 |

Unit Cell Constants

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| a | 9·15 | 9·19 | 9·20 | 9·188 | 9·202 | 9·202 | 9·200 |
| c | 9·21 | 9·17 | 9·21 | 9·189 | 9·183 | 9·209 | 9·227 |
| c/a | 1·006 | 0·998 | 1·001 | 1·000 | 0·998 | 1·0008 | 1·003 |
| Specific Gravity | 2·71 | 2·70 | 2·84 | 2·71 | 2·72 | 2·75 | 2·78 |

1. Clear light blue core zone of Mt. Marion beryl, Western Australia.
2. Cloudy white margin of Mt. Marion beryl, Western Australia.
3. Light pink beryl from Wodgina, Western Australia.
4. Clear light green beryl from Yinnietharra, Western Australia. (Norrish 1950.)
5. Green beryl from pegmatite, U.S.S.R. ⎫
White beryl from pegmatite, U.S.S.R. ⎬ Sosedko T.A. (1957).
nk beryl from pegmatite, U.S.S.R. ⎭

process of crystallising. So that while at Wodgina the residuum was essentially fluorine-rich, at Mt. Marion it was correspondingly siliceous.

Although the cloudy white nature of some Mt. Marion beryl is readily explained through late stage kaolinisation, the pink and blue colours of the remaining two varieties is not so readily understood. Nevertheless, it is considered that these characteristics may arise through the contrasting distribution of trace elements; the pinkish hue being due to the presence of cobalt and manganese, and the blue probably to chromium. An additional factor, particularly in the pink Wodgina beryl may be the anomalous refraction effects produced by its minute fluorite inclusions.

## Acknowledgments

For critical reading and comments of this note the writer is indebted to Mr. A. J. Gaskin, Chief of Division of Applied Mineralogy, C.S.I.R.O.

The partial chemical analyses of the new varieties of beryl were carried out by Mr. T. H. Donnelly, to whom much thanks is due.

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# 9.—Contributiones Florae Australiae Occidentalis XIII

By C. A. Gardner[*]

*Manuscript received—16th July, 1963*

Descriptions are given of 35 species previously undescribed. They have been selected from a large number of plants awaiting description because of their more than usual interest. The *Actinostrobus* has for long been confused with *A. pyramidalis*, and is by far the most widespread species of this endemic genus; the *Casuarina*, a plant of unusual habit within the genus is of very localised occurrence. The seventeen Proteaceae have been included since they will be incorporated in that portion of the "Flora of Western Australia" nearing completion. During the preparation of this work it was found that considerable confusion existed in the genus *Dryandra*, of which five new species are now described. Of the species of *Banksia*, one (*B. pilostylis*) has been confused with *B. media*, while the species of *Grevillea* are from localities previously little known botanically.

Two species of the Papilionaceae are included because they belong to the toxic sections of *Oxylobium* and *Gastrolobium* the latter being already a confirmed toxic species, and the former will prove to be so.

In the Myrtaceae two species of *Eucalyptus* are described; one from Kimberley apparently has a restricted range while the other species has been confused with a form of *Eucalyptus eudesmioides*, but with which it has no true affinity. One new *Regelia* is described, and the names of two well-known species have been changed in accordance with International Rules. The two species of *Wehlia* are perhaps the most attractive of the genus, and both are from the Eremaean Province. The species of *Darwinia* bears a strong affinity to a South Western species, but grows in the Eremaea.

In the Chloanthaceae are three spectacular plants, a *Lachnostachys*; a *Newcastlia* with extraordinary foliage, and also of tall erectly branched habit, its golden-tomentose leaf undersurfaces making it at once a plant of singular attractiveness; and thirdly the most showy of the species of *Pityrodia*, named *P. spectabilis*, a species in danger of extinction owing to agricultural extension in the area in which it grows.

In the Labiatae is a small compact rare *Prostanthera* with pale blue flowers.

In the Goodeniaceae, a cushion-like *Leschenaultia* with pale blue corollas and a white throat is described together with a magnificent biennial *Goodenia* with long spike-like inflorescences, the flowers almost hidden in the dense silk of the spikes.

*Leptospermum sericeum*, for many years regarded as synonymous with *Kunzea sericea*, has been restored as a valid species; it has been included for its undoubted horticultural value, and is probably the largest-flowered and most attractive species of this genus in Australia.

## CUPRESSACEAE

**Actinostrobus arenarius** C. A. Gardn. sp. nov.

Frutex 2-5 m. altus, ramis plusminusve divaricatis, rigidiusculis, ramulis triquetris; folia ternata, squamiformi-triquetra, ad basin adnata, sursum patula. parte libera late ovata, acuta. Amenta mascula ignota. Strobili foeminei manifeste pedicellari, pedicelli squamis abbreviatis appressis obtecti; strobilus ovoideo-globosus, breviacuminatus, squamis exterioribus vacuis, tenuibus, parum auctis, arcte appressis, interiores gradatim majoribus, ovatis, marginibus tenuis; squamis fertilibus induratis, ovato-lanceolatis, in apicem attenuatae erectis; semina magna, pauca, 2- vel 3- alata, luteo-brunnea.

Hab. in regionibus interioribus arenosis; stationes maxime australes a flumine Murchison usque oppidem Bruce Rock valde insignis, occidentalem versus Darling Range non transgrediens; frequenta occurrens in distr. Irwin et Avon in arenosis apertis. Typus prope Tammin, *Gardner* n. 610. Novem. 1920.

Formerly included with *A. pyramidalis* Miq. this species remains distinct in the more glaucous foliage and cones, the fertile scales of which have erect and somewhat acute, not incurved apices, they are also larger, and glaucous, the leaves of *A. arenarius* are ovoid-deltoid in the free portion, whereas in *A. pyramidalis* they are ovate and more spreading.

Leaves mostly 2 mm. long, the free part slightly less than 1 mm.; cones 1.5-1.6 cm. long, 1.6 cm. broad; seeds 1.1 cm. long.

## CASUARINACEAE

**Casuarina ramosissima** C. A. Gardn. sp. nov.

Frutex probabiliter dioicus, usque 1 m. altus, ramis ramulisque subconforibus, numerosis, verticillato-ramosis, ramulis 2-3- articulatis, cinereo-tomentosis, fere rigidis, patentibus, glaucis, profunde sulcatis demum glabris; internodia (basalia excepta) 1-2 cm. longa, dentes 4, erecti, deltoidei, obtusi, ciliati, apice nigri. Amenta mascula ignota. Strobilis sessilis, verticillatis vel oppositis, breviter cylindricis vel ovoideo-cylindricis, basi truncatis, circ. 1 5 cm. longis et 1 cm. latis; bractea magna late ovata, dorso rufo-tomentosa, apicem versus in appendicem contracta, apice late ovata, atro-fusca marginibus fimbriolata; bracteolae basi connatae, vix exsertae, dorso lato verrucoso areolatae et dense fibroso-piloso; achaenia atro-fusca, crassa vel turgida et breviter pilosa, ala obliqua, vix scariosa.

Hab. in distr. Avon prope Dandarragan, in arenosis glareosis in fruticulosis, *Gardner* 9013, (TYPUS).

In its compound branchlets this species is related to *C. microstachya* Miq. and *C. Drummondiana* Miq., all the remaining species having undivided branchlets. From *C. microstachya* it differs in its taller stature, longer ashy-tomentose branchlets, very different bracts, and sulcate. not tetragonal internodes. From *C. Drummondiana* it can be distinguished by the much longer, not glabrous internodes, larger fibrous-hairy bracteoles and darker coloured, less hairy and shorter winged achenes.

## PROTEACEAE

**Conospermum sericeum** C. A. Gardn. sp. nov.

§*Euconospermum* Benth.

Fruticulus vel suffrutex habitu simile *C. coeruleum*, cauli scapiformi, basi folioso sericei, superne aphylli, dichotomoso-ramoso vel scapi-

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[*] Herbarium, Western Australia.

formi; folia erecta, lingulata elongata, usque 12 cm. longa, uninervia, nervoso-marginata, glabra, infra medium attenuata in petiolum basi dilatata, acuta apicibus ustulata.

Spicae breves, fere in capitulum, contractae, multiflorae, longe pedunculatae folia longe superantes et quasi corymbum floriferum pulchrum constituentes; bracteae florigerae lanceolatae basin versus attenuatae, in apicem acuminatae productae cymbiformae, subtus et marginibus sericeis, pallide coeruleae, perianthio subaequales.

Perianthium 4 mm. longum, pulchre coeruleum, tubum glabrum, limbi labium superius integrum, leviter concavum dorso breviter hirsutum, acutum, marginibus elegante ciliatum; labium inferior profunde trilobum, lobi anguste lanceolati, acuti, marginibus longe ciliati, dorsale pilosi.

Hab. in distr. Irwin prope flumen Hill juxta Badgingarra in arenosis apertis, flor. m. Decembri. *F. Lullfitz* n. 2156 (TYPUS).

The affinity of this species is with *C. coeruleum* Meissn. and *C. debile* Kipp. differing from the former in the narrow cymbiform not woolly bracts and the densely ciliate lobes of the lower lip, and from the latter in much longer obtuse leaves, and the indumentum of the flowers.

### **Lambertia orbifolia** C. A. Gardn. sp. nov.

Frutex 2-2.5 m. altus, ramis ramulisque erectis, villoso-tomentosis pilisque longis intermixtis, pilis patentibus. Folia opposita, erecto-patula, sessiles, orbiculares, integra, basi cordato-orbiculares, subcucullata, conspicue penninervosa et reticulata, 2 cm. longa, 1.8 cm. lata. Involucri 4-6 flori, axillares vel ramulis terminati; bracteae exteriores oblongo-ovatae valde obtusae vel truncatae, dorso dense tomentosae, interiores multo longiores sed similes.

Perianthium rubrum, 4.7 cm. longum; segmenta basin attenuata, superne dilatatà et leviter curvata, sursum contracta et spiraliter revoluta (obtorta) et hirsuta, limbum angustum, erectum, breviter hirsutum, apicibus breviter barbatis; squamae hypogynae lineari-lanceolatae, acuminatae, liberae. Ovarium longe et dense pilosum; stylus filiformis.

Hab. in distr. Stirling haud procul King George's Sound, juxta flumen King, in arenosis glareosis in fruticetis, fl. m. Junio, leg. *A. J. Gray* (TYPUS).

Differs from all other species in the orbicular cordate leaves, but closest to *L. inermis* R. Br., from which it differs in the larger hairy perianth, the narrower truncate bracts, and much broader sessile leaves.

### **Grevillea globosa** C. A. Gardn. sp. nov.

§*Plagiopoda*.

Frutex erectus usque ad 2 m. altus, ramis ramulisque erectis, ramulis juvenilibus sericeo-pilosus. Folia erecta, pinnatisecta, 7-9-fida, lobis tenuis sed rigidis, anguste linearea vel subteretia, leviter pubescentibus, subtus bisulcatis, demum glabrescentibus, glaucis.

Racemi terminali, breviter pedunculati foliis multo breviores; pedunculi rufo-tomentosi; pedicelli 4 mm. longi: sericei. Flores zygomorphicum racemo terminali. Perianthium rubrum, basi dilatatum, segmenta perangusta, lineari-oblonga, extus sparse sericeo-villosa, sursum attenuata, sub limbo globosa revoluta, intus glabra, extus in partis inferioribus sparse sericeo-villosa, limbo albo-villoso. Torus obliquus; glandula hippocrepiformis, plana; ovarium dense villosum, stipite ovario longiore; stylus 17 mm. longus, parte inferiore sparse hirsutus, ceterum glaber, curvatus, disco stigmatico orbiculari, laterali terminatus. Fructus ignotus.

Hab. in distr. Austin, Pindar 32km. septentrionalem versus juxta confragosos lateritos, fl. m. Januario. *F. Lullfitz* n. 2241 (TYPUS).

The affinity of this species is with *G. tenuiloba* C. A. Gardn., from which is differs in the much longer leaves with more numerous segments, the short ± globose racemes and conspicuously silky perianth-limb.

### **Grevillea ninghanensis** C. A. Gardn. sp. nov.

Frutex nanus, usque ad 20 cm. altus, crebre divaricato-ramosa, ramulis appresse-pubescentibus. Folia fasciculata, subsessilia, in ramulis patulis disposita, coriacea, viridia, linearia, 1-1.6 cm. longa, mucronato-pungentia, basi sensim attenuata vel subsessilia, marginibus valde revolutis, glabra, supra convexa et laevia, subtus bisulcata.

Racemi axillari, laxissimi, secundi, 2-4 cm. longi, rhachis sparse pubescentibus, pedicelli 2-3 mm. longi, appresse-sericei, perianthii tubus 10-11 mm. longus, sub limbo parvo globoso revolutus, segmenta perangusta, basi dilatata, extus sparse appresse-sericea, intus parte media sparse appresse-sericea, superius glabra; torus obliquus, fere orbiculatus; ovarium dense sericeum, stipitatum; stylus circ. 12 mm. longus; basin versus crassus, glaber, apice recurvatus, disco stigmatico orbiculari, laterali terminatus; glandula semilunaria, parvum prominens.

Hab. in distr. Austin, prope Ninghan, in acacietis in argillaceis fl. m. Aug. *Gardner* n. 12502 (TYPUS).

This species is related to those of the Section *Plagiopoda* which have entire leaves with closely revolute margins, and loosely racemose flowers. It differs from *G. deflexa* in having narrower, shorter and more closely revolute leaves, erect racemes, and shorter styles. It is also a much smaller shrub with the branches close to the ground.

### **Grevillea fulgens** C. A. Gardn. sp. nov.

§*Plagiopoda* Benth.

Frutex 90 cm. altus, ramis divaricatis vel erectis, subflexuosis, ramulis saepe erectis, juvenilia pubescentia.

Folia erecto-patentia, linearis, basi attenuata, breviter petiolata, obtusa, rigide mucronulata, 7-8 cm. longa, integra (vel rarius 2-3 loba lateralia nascentes) marginibus arcte revolutis, supra glabra, unisulcata, subtus bisulcata.

Flores zygomorphi, in axillis foliorum singuli vel bini, et ramulis axillaribus terminantae; pedunculi appresse villosiusculi circ. 5-7 mm. longi, bracteati, bracteae exteriores lanceolatae, brevae, interiores magnae, 2, obovato-cuneatae truncatae, vel breviter dentatae, mucronatae, dorso ferruginoso-tomentosae, sursum glabrae, alabastri includens; pedicelli rufo-hirsuti, 5-6 mm. longi.

Perianthium scarletinum lilacino-suffusum, sub limbo globoso recurvum, torus obliquus; segmenta basi dilatata, extus (limbo excepta) glaber, tubus parte basali extus sparse hirsuta, cetera glabrus; limbus apicem versus sparse hirsutus; glandula hippocrepiformis; ovarium stipitatum, dense albo-pilosum, stipite ovario paulo breviore; stylus crassus, fere rectus, circ. 2 cm. longus, laxe et appresse pilosus, disco stigmatico orbiculare, laterali.

Fructus rectus, ovoideo-oblongus, glabrus, 1-2 cm. longus styli longe persistens basi coronatus.

Hab. in distr. Eyre montem Desmond ad collis latera petraea, in fruticulosus densus, fl. m. Aug-Septem. *Gardner* 14070 (TYPUS) etiam 13718, 12883.

Although the position of the torus is that of the species of the Section *Plagiopoda*, it has no close affinities within this Section, nor with the species of the Sect. *Hebegyne*. It has the bracts, leaves and fruit of *G. bracteosa* Meissn. but is otherwise unrelated.

### **Grevillea candelabroides** C. A. Gardn. sp. nov.

*§Cycladenia*

Frutex vel arbor usque 5 met. alta; rami patenti vel erecti, primum pubescentes demum glabrescentes. Folia alterna, pinnatisecta, segmenta 8-9, lineari-filiformia, compressa, acuta, glauca, subtus bisulcata, 8-13 cm. longa, in toto usque 20 cm. longa.

Racemi numerosi, stricte erecti, in paniculam dispositae, breviter pedunculati, folia excedenti; pedunculi atro-purpurascenti, usque 5-6 cm. longi; pedicelli 4 mm. longo, glabri.

Perianthium extus glabrum, intus sub medio barbatum ceterum glabrum, tubum sub limbum rovolutum; torus rectus; glandula hypogyna annularia, subcupulari, ovarium glabrum, longe stipitatum; stylus 8-9 mm. longus, glaber, disco stigmatico obliquo in truncatum coronatum attenuatum.

Fructus oblique ovoideus, compressus, sublaterali affixus, brunneus vel pallidus, saepe apice subulato curvatus (basi styli persistente) ad 1.3 cm. longus; semina subovalia, compressa, circ. 1 cm. longa, grisco-viridia, undique latius alata.

Hab. in distr. Irwin interiores, prope Mingenew et Indarra septentrionalem versus extendit ad super flumine Murchison, distr. Austin regionem invadit, in fruticetis fl. m. Decembri et Januario, *Gardner* 12312; in arenosis apertis prope Ajana *Gardner* 12062 (TYPUS).

The species is related to *G. leucopteris* Meissn., differing in the spruce-like compact habit, the strictly erect candelabra-like panicles of racemes which are both erect, the glabrous branchlets, almost sessile racemes which scarcely exceed the leaves, the glabrous and somewhat viscid fruit and the presence of an oblique truncated stigmatic cone. It flowers in summer, whereas *G. leucopteris* blossoms in September and October.

### **Grevillea Gordoniana** C. A. Gardn. sp. nov.

*§Cycloptera*

Frutex elatus subarborescens usque 7 m. altus, ramis ramulisque erectis, ramulis appresse-pubescentibus.

Folia erecta, densa, sparsa, integra, rigida, teretibus, juvenilis rufo-tomentulosa, exsulca, breviter acuta vel mucronata, apicem ustulatum.

Panicula ampla, terminalis, speciosa, e racemis numerosis, breviter pedunculatis, densifloris, subglobosis, composita; pedunculi 3-6 mm. longi; pedicelli gracili, glabri, 6-7 mm. longi; bracteis aurantiaco-tomentosis, obtusis, diu persistentibus, late ovatis, vel orbicularibusve, unguiculatis, erectis, intus glabris.

Perianthium luteum, 7-8 mm. longum, sub limbo globoso revolutum; torus rectus, cupulatus, segenta (valde inaequalibus) basi dilatata, extus glabra, intus parte basali dense barbata, superius glabra; glandula hypogyna cupulata; toro adnata; ovarium glabrum, stipitatum, stipite ovario longiore, glandula marginibus inserta; stylus 7-8 mm. longus, glaber, apice breviter recurvatis et disco stigmatico magno orbiculari terminatus, in centro umbonato.

Fructus elongatus, anguste-oblongatus, sinuatus, 2 cm. longus, obliquus, verrucosus et viscidus; semina lineari-sigmoidea, undique latius alata.

Crescit in district Austin flumen Murchison 40km. septentrionalem versus in lutoso arenosis in fruticetis, fl. m. Decem. *Gardner* 14273 (TYPUS).

It is difficult to place this anomalous species in any given Section of the genus. The lateral umbonate stigmatic disc is not in conformity with the Section *Cycloptera*, but the inflorescence being paniculate, and the cupular torus lined by the disc appear to warrant its retention with the Section. The peculiar fruits which do not freely emit the even more peculiarly shaped seeds are without parallel in the genus. The very short rhachis and subumbellate inflorescence, the dehiscence of the perianth segments above the actual base of the perianth, and the orbicular tomentose bracts are certainly without parallel in the section *Cycloptera*, but the attachment of the ovary stipes to the disc margin make it impossible of insertion in the Section *Cycladenia*.

This remarkable plant commemorates the name of Mr. D. N. Gordon of Myall Park, Glenmorgan, Queensland, who has cultivated numerous Western Australian plants in his garden, and who was instrumental in providing the first specimens of this species through one of his collectors (Mr. A. J. Gray).

### **Grevillea Rogersoniana** C. A. Gardn. sp. nov.

*§Anadenia*

Arbor vel frutex usque 8 m. alta, ramis erectis vel erecto-patentibus, crebo foliatis, ramulis teretibus.

Folia petiolata, oblongo-spathulata, basin versus sensim attenuata, integra vel cuneata et bi- vel triloba, lobis ovato-triangularibus, obtusis vel calloso-mucronatis, plana, laevia, glauco-viridia, trinervis vel quinquinervis, omnino glabra.

Racemi numerosi, densiflori et multiflori, in paniculis terminalibus dispositi, 7 cm. longi; pedunculi sparse appresso-sericei. Flores regulares, breviter pedicellati, pedicelli 1 mm. longi.

Perianthium roseum, 8.10 mm. longum, rectum, limbo anguste-elliptico, segmentis filiformis, basi haud dilatatis, extus et intus glabris; torus rectus; glandula hypogyna parva, semiannularia, parum prominens. Ovarium glabrum, stipitatum, stipite 2 mm. longum; stylus circ. 1 cm. longus conico-stigmatico recto, basi marginato.

Fructus ovoideo-globosus, dense resinoso-tuberculatus, mucronatus, leviter compressus, valvulis crustaceis. Semina 2, elliptico-hemispherica, alba, laevia, exalata, 1.5 cm. longa, 11-12 mm. lata.

Hab. in distr. Irwin septentrionalem versus ad Shark Bay, in arenosis fruticetis, fl. m. Aug. Septem. *Gardner* 13517 (TYPUS).

Affinity with *G. petrophiloides* Meissn., from which it differs principally in the greater size, more robust habit, the flat entire or simply lobed leaves, the lobes being broad and flat, also in the larger more verrucose fruits which, although viscid have much smaller resinous cavities and smaller tubercles than is the case with *G. petrophiloides*. *G. petrophiloides* sometimes has flat-leaf-segments, but these are always narrow and proportionately very much longer and always linear.

The species commemorates Mrs. W. Rogerson of Gosnells who first directed my attention to this handsome species.

### **Hakea tamminensis** C. A. Gardn. sp. nov.

§*Euhakea* Benth.

Frutex horridus, 2 m. altus, crebo ramosus, ramis divaricato-ramosis et intricatis, ramulis tomentoso-villosis.

Folia alterna, lineari-teretia, divaricato-patentia, vel inferiores erecta, rigida, coriacea, stricta, glabrescentia, 5-6.5 cm. longa, basi non contracta, apice rigide pungentia.

Racemi ad umbellas redacti, axillari, multiflori; breviter pedunculati, foliis multo breviori; bracteae ovatae, glabrae, stipitatae; pedicelli 4 mm. longi, dense hirsuti. Floribus purpureis vel rubris.

Perianthium sub limbo parvo globoso revolutum, 4-5 mm. longum, segmenta lineari-oblonga, basi haud dilatata, extus sparse hirsuta, intus glabra. Torus parvus, rectus; glandula hypogyna erecta, hemisphaerico-truncata, parum prominens; stylus breviter exsertus, glaber, apicem versus incrassatus, disco stigmatico laterali terminatus.

Fructus valde obliquus, crassus, ovoideus, brevi crassique pedicellatus, 3.5 cm. longus, 2.5 cm. latus, gibbosus, prominenter et longitudinaliter cristatus et supra profunde sulcatus; semina obovata ala ovato-oblonga, secus marginem basique decurrente, hinc paulo valde atra rugulosa.

Hab. in distr. Avon prope Tammin in arenoso glareosis, fl. m. Julio-Aug. *Gardner* n. 11997 (TYPUS).

Affinity with *H. circumalata* Meissn., from which it differs principally in the densely hirsute pedicels and the cristate, deeply and broadly sulcate fruit.

### **Banksia laricina** C. A. Gardn. sp. nov.

§*Oncostylis*

Frutex circ. 1 m. altus, ramis erecto-patentibus, ramulis cano-puberulis. Folia linearia, circ. 1.5 cm. longa, distincte petiolata, mucronata, supra viridia et laevia, marginibus arcte revolutis, subtus unisulcatis vel canaliculatis.

Spicae pedunculatae, ovoideo-globosae vel breviter cylindricae, 2.5-3 cm. longae; bracteae crassae, cuneatae, rufo-villosae, truncatae, apicibus albo-tomentosae.

Perianthium luteum, appresso-sericeum, sub limbo ellipsoideo reflexum, 1.3 cm. longum, limbo 3 mm. longo; stylus glabrus tenuis sed rigidus sursum hamosus, perianthio multo longior arcuatim exsertus, conico-stigmatico atro, brevi, exsulcato. Conus fructifer, 5 cm. longus, 8.5 cm. latus; folliculi lignei, glabri et prominentes, valde exserti, 3.3-3.5 cm. lati, marginibus tenuis et aliquando undulatis.

Hab. in distr. Darling prope flumen Moore et Beermullah, in arenosis depressis subhumidis, fl. m. Jun-Julio, *Gardner*, 12840 (TYPUS).

The affinity is with *B. nutans* R. Br., but the bracts are white-tomentose at the truncate tips, the cones erect, and the follicles are entirely different, being much exserted without any persistent perianths surrounding them, are much broader and with thin margins, entirely unlike those of any other species of the genus.

### **Banksia pilostylis** C. A. Gardn. sp. nov.

§*Cyrtostylis* Benth.

Frutex 2-3 m. altus, ramis ramulisque erecto-patentibus, ramulis cano-tomentosis.

Folia sparsa, petiolata, patentia, linearia, truncata, remote serrato-dentata, basi attenuata, 9-12 cm. longa, 12-15 mm. lata, dentibus rigidis, acutis marginibus recurvis, supra laevia glabra, nitentibus, subtus costato-reticulata lacunis albo-tomentosis, tantum conspicuis punctata, venulis glabratis.

Spicae ramis terminatae, cylindricae, 5-10 cm. longae, erectae, densiflorae.

Perianthium pallide luteum in vetulis demum luteo-brunneum, dense villosum; limbo elliptico, acuto, densissime villoso, limbo obtuso, 4 mm. longo, apicibus ipso glabro; stylus arcuatus, rigidus, laxe pilosus, perianthium paulo excedens, cylindrico-stigmatico vix latiore, brevo, sulcato terminatus.

Folliculi transversi, glabri, obtusi, rufo-brunnei, cum pallide luteo maculati, 2 cm. lati, dorso convexi.

Hab. in distr. Eyre in arenosis inter flumina Oldfield et Young septentrionalem versus ad collibus "Fitzgerald Peaks" in arenosis dunosis fruticetis, etiam prope Starvation Boat Harbour, fl. m. Oct. *Gardner* 12149 (TYPUS).

The fact that this species is so common within the area given above, suggests that it has not been overlooked, and must have been seen and collected by Baxter and Maxwell. It has a certain resemblance to *B. media* R. Br., but the leaves are much longer and more white underneath, and the spikes are also narrower and longer. The hirsute style is quite distinct from *B. media*. It is possible that Bentham included this species with *B. media* notwithstanding the difference in shape, size and indumentum of the lower leaf surface (*B. media* having always much shorter and relatively broader leaves almost glabrous underneath, a perianth which has a much shorter indumentum, and the limb of which is soon glabrous). The style is glabrous, and the spike much shorter and thicker. The two species are entirely distinct.

### **Banksia Benthamiana** C. A. Gardn. sp. nov.

§*Cyrtostylis* Benth.

Frutex erectus, usque 4 m. altus, ramis erectis, ramulis brevibus, patentibus, cano-tomentosis.

Folia erecta, rigida, elongato-linearia, usque 19 cm. longa et 6-7 mm. lata, utrinque glabra, subconcolorata, apice breviter acuta, sursum ultra medium remote dentata, dentibus acutis, deltoideis, sinubus costa media parallelis, in sicco utrinque luteo-viridia, pagina superiore enervia, laevia, subnitidula, subtus simulate glabra et haud nitidula et lacunis albido-tomentosis praeditis, tantum sub lente conspicue parce punctata, marginibus crassa in petiolo brevi sensim attenuata, costa media supra prominula immersa, subtus crassa.

Spicae densae ramulorum terminantibus erectae, cylindricae, 7-9 cm. longae, usque 6 cm. latae, folia pauca obvallata: bracteae pubescentes, patulae, rufo-barbatae.

Perianthium aurantiacum, 2 cm. longum, adpresse flavido-sericeum, laminae lineari-lanceolatae, 5 mm. longae. Stylus rigidus, rectus, demum sursum leviter curvatus perianthio leviter longior; stigma 4 mm. longa, stylo glabro haud crassior sed basi constricta ab eo distinctum continuum attenuatum, laeve.

Folliculi parvi, transversi 12 mm. lati depressi tomentosi, perianthiis marcescentibus obtengentibus.

Hab. in distr. Austin ab Dalwallinu ad lacum Monger, attingit et prope oppidulum Wilroy, in arenoso glareosis, fl. m. Decembri-Januario, prope Wubin *Gardner* 12097; Wilroy *Gardner* 12075 (TYPUS).

The species is related to *B. Elderiana* F. Muell. et Tate, but can be distinguished by the vesture of the perianth, as well as by the longer erect flowering spikes, and the narrower sulcate stigmatic cone. It is also a larger shrub.

### **Dryandra cynaroides** C. A. Gardn. sp. nov.

§*Eudryandra* Meissn.

Frutex erectus, 1-1.3 m. altus, sparse ramosus, rami erecti, dense villosi; rami juveniles inter folia squamis lanceolatis tectis. Folia subverticillata, lineari-lanceolata in circuitu, in petiolum longum angustata, apice pungentia, subpinnatifida; lobis remotis et lanceolato-triangularibus, erecto-patentibus, pungentibus, marginibus recurvis, sinubus latis et ad costam mediam parallelis; supra glabra laeviaque, nervis prominentibus, subtus albo-tomentosis, costa media prominenti.

Capitula sessilia, terminalia, solitaria, saepe ramulis lateralis abbreviata terminantia, foliis floralibus obvallatis; involucra permagna usque 3 cm. expansa; bracteae numerosissimae, exteriores lineari-filiformes, interiores setaceae, plumosae, ciliatae, exterioribus longiores, omnes apicibus plumosae.

Perianthium supra basin glabrum, turgidum et dense sericeo-tomentosum, segmentis fere medium cohaerentia, sursum breviter tomentosa, deinde glabra, laminae profunde sulcatae, glabrae, angustae; stylus perianthio vix excedens, rectus, glaber; cylindrico-stigmatico vix latiore terminatus.

Hab. in distr. Avon Pingelly orientalem versus, in arenosis lateritis, fl. m. Novem. *Gardner* 14255 (TYPUS).

The affinity is with *D. erythrocephala* C. A. Gardn., from which it differs in the longer perianth 5.5 cm long, the much shorter broadly lobed leaves with recurved (not revolute) margins, and the elegantly ciliate bracts and glabrous style, etc. The flowers are yellow.

### **Dryandra subpinnatifida** C. A. Gardn. sp. nov.

§*Eudryandra* Meissn.

Fruticosa 1.5 m. alta, crebre virgato-ramosa, ramis erectis, glabra, insuper pluriramosa, ramulis brevibus, patentibus, conferte foliosis; folia linearia, usque 23 cm. longa, infra media spinoso-pinnatifida, rhachi vix 1 mm. lata, lobis patentibus, anguste-triangularibus vel linearibus, spinescentibus, sinubus rectangulariter dispositis, sursum linearia, integra (inusitate sparse lobata) lobis acutis, 4 mm. lata, supra glabra et laevia, costa media impressa, subtus niveo-albo tomentosa, marginibus recurvis, costa media prominentibus.

Capitula terminantia et praecipue copios ramulos laterales florentibus foliis numerosis obvallatis capitula manifeste excedentibus; involucrum turbinatum cum bracteis numerosissimis quorum exteriores foliolatis, interiores lanceolato-linearibus, acuminatis, omnes apicibus patulae et glabrae.

Perianthium circiter 3 cm. longum, inferius tomentosum ipso basin costatum glabrum, sursum sericeo-villosum, limbus obtusus, plumosus; stylus glaber, perianthium excedens, rigidus, cylindrico-stigmatico anguste conico.

Crescit in distr. Stirling, Popanyinning occidentalem versus in collibus glareosis, fl. m. Septem. *F. Lullfitz* (Typus).

The affinity of this species is with *D. squarrosa* R. Br. from which is differs in the much larger perianth and entirely different foliage which has no similarity to any other species of the genus. The flower-heads of *D. squarrosa* are described as being axillary; those of *D. subpinnatifida* are terminal.

### **Dryandra foliosissima** C. A. Gardn. sp. nov.

§*Eudryandra* Meissn.

Frutex erectus, usque 2 m. altus, dense ramosissimus, ramis ramulisque brevibus, patentibus. Folia densa, patentia vel recurva, usque 23 cm. longa, linearia, marginibus recurvis, pinnatifida, acuta, lobis brevibus, remotis, deltoideis, patentibus, mucronulatis, breve-decurrentibus, 2-3 mm. longa, vix 3 mm. lata, sinubus latis, costa media parallelis, supra viridia et glabra, costa media prominula immersa, subtus costato-reticulata, sordide albo-tomentosis.

Capitula ramos et ramulos laterales copiosos terminantes expansa ad 4.5 cm. diam., foliis numerosissimis capitula longe superantibus; involucri turbinati, bracteae exteriores lineari-subulatae, appressae, interiores latiores et rufo-tomentosae, omnes acuminatae et erectae.

Perianthium circ. 2.5 cm. longum, ad basin costatum sericeo-hirsutum, supra dense tomentoso-lanosum, sursum (unguibus) sparse-pilosum, limbo angustissimo extus apicem versus sericeo-barbato. Stylus glaber, perianthium paulum excedens, cylindrico-stigmatico non latiore terminatus. Folliculis obovoideis, dense rufo-tomentosis vix compressis, 1.4 cm. longis 7-8 mm. latis.

Hab. in distr. Eyre in saxosis in fruticetis, summo montem Desmond prope Ravensthorpe, in fruticetis densis, fl. m. Junio et Julio, *Gardner* 12886 (TYPUS).

This species has a close affinity with *D. mucronulata*, R. Br., with which is has been confused. It agrees in many respects with the description given by Bentham in the Flora Australiensis, but there are several small, but important differences.

*D. mucronulata* has flat leaves which are divided almost to the midrib, the lobes being triangular and acute or finely mucronate, and the sinuses are acute. The inner bracts are obtuse and mucronate. In *D. foliosissima*, which apparently has the same habit as *D. mucronulata*, the sinuses are very broad and parallel to the midrib, the leaves very much longer, the margins strongly recurved, and the teeth much smaller. The bracts are all acute or acuminate. It appears to be restricted to the vinicity of Mount Desmond, whereas *D. mucronulata* would appear to be restricted to the vicinity of King George's Sound and the Stirling Range. *D. foliosissima* appears to be still more closely related to *D. squarrosa* R. Br., of which I have not seen specimens. The fragment in the Melbourne Herbarium doubtfully referred to as *D. squarrosa* by Bentham is *D. polycephala*. From the description given of *D. squarrosa*, the involucres would appear to be very different from those of *D. foliosissima*.

### **Dryandra subulata**, C. A. Gardn. sp nov.

§*Acrodontae* D.C.

Fruticulus humilis 30-35 cm. altus, ramis stricte ascendentibus, juvenilibus tomentosis vetulis glabratis; folia erecta, anguste-linearia, plerumque 25-30 cm. longa, 1.5-2 mm. lata, integra, margine crasso arcte revoluta, in petiolum breviter attenuata (ipso basin subdilatatum) longiuscule mucronato-spinescentia juvenilia sparse sericeo-puberula, adulta demum glabra, subtus bisulcata, sericeo-tomentosa.

Capitula subsessilis, ramos et praecipue ramulos laterales copioso terminantia, expansa usque 2.5 cm., foliis mumerosis capitula multo superantibus obvallata; involucri late turbinati; bracteae numerosissimae, exteriores lineari subulatae, usque 5-6 cm. longae, basi dilatatae, viscideae, interiores breviorae, omnes rectis et apicibus subulatae.

Perianthium ca. 2 cm. longum, basin brevem glabrum, sursum tomentoso-villosum, limbum glabrum, tubum sursum attenuatum et glabrum; stylus rectus glaber, perianthium non exceedens; cylindrico-stigmatico atro-fusco, leviter sulcato.

Hab. in distr. Irwin prope flumen Hill, in fruticetis apertis in arenoso-glareosis, fl. m. Septem. *Gardner* 12175 (TYPUS) etiam locis eisdem, *A. J. Gray*.

This species differs from the others of this Section in habit, in the exceptionally long entire linear leaves none of which closely surround the flower-heads, the heads being surrounded by external subulate bracts which are almost three times longer than the involucre proper.

### **Dryandra arborea** C. A. Gardn. sp. nov.

§*Eudryandra* Meissn.

Arbor usque 5 m. alta, ramis patentibus, trunco usque 30 cm. diametri, cortice nigra; ramulis brevibus ad apicem solum foliolatis; folia petiolata, oblanceolata, plana, subpinnatifida, basi cuneata, lobis patentibus, triangularibus, decurrentibus, pungentibus, subtus reticulatis, glaucis, subalveolatis, sinubus acutis; capitulis terminalibus, involucro floribus multo breviore, squamis (bracteae) glabriusculis ciliatis, lanceolatis, acutis, demum glabrescentibus.

Perianthium stylum subaequantum, unguibus dense tomentosum; stylus breviter exsertus, basi lanuginosus; stigmatico cylindrico obtuso.

Folliculi oblique ovati, biconvexi, glabriusculi demum glabri, reticulato-striati, margine acuto compressi.

Hab. in distr. Coolgardie in rupestribus "Iron Knob", collibus Koolyanobbing, fl. m. Oct. *Gardner* 12217 Oct. 1959 (TYPUS).

This species was previously collected by Young between Ularring and Mount Churchman, and also by John Forrest, and was named *D. armata* by Mueller, although it has very little in common with the latter, apart from the woolly base of the style. The involucral bracts are quite distinct from those of any other related species, and the floral leaves are not obvallate. It is also the only arborescent species of the genus known to me. *D. armata* R. Br. (*sensu strictu*) is confined to the south coastal areas, and may be easily distinguished by its hirsute branchlets, long hairy and long-ciliate bracts, and in addition these latter always have nigrescent-tomentose apices, a characteristic confined to this and the closely related *D. Purdicana* Diels and *D. Gilbertii* S. Moore.

## PAPILIONACEAE

### **Oxylobium rigidum** C. A. Gardn. sp. nov.

§*Podolobium*

Frutex humilis, usque 30 cm. altus, glaber; ramis erectis; ramulis angulosis. Folia opposita, breviter petiolata, oblongo-lanceolata, plana, rigida, costa media prominens, basi leviter sed conspicue cordata, apice acuta, subpungentia, glauca; stipulae setaceae, nigrae, petiolis longiores. Flores pauci ad ramulorum apices in racemos pedunculati, verticillato-dispositae, pedicelli circ. 1.5 mm. longi; bracteolae deciduae. Calyx coriaceus, circ. 6 mm. longus, campanulato-cupuliformis, glaberrimus, glaucis, lobi 3 inferiores ovato-lanceolati, circ. 2.5 mm. longi, tubo breviores, lobis superioribus approximati, altius connati, truncati, marginibus ciliolati; vexillum calyce haud duplo longior cordato-emarginatum, alae vexillo paulo breviores, obtusissimae; carina aliis multo longior; ovarium longe stipitatum; villosum 4-ovulatum.

Hab. in distr. Eyre montem Madden septentrionalem versus, in glareosis fruticetis, fl. m. Oct. *Gardner* 13635 (TYPUS).

The affinity of this species is with *O. racemosum* (Turcz.) C. A. Gardn., from which it differs in the usually acute leaves, the shorter pedicels, upper ciliolate calyx-lobes silky ovary, and number of ovules, and the much more rigid glaucous foliage with scarcely evident venation. *Oxylobium racemosum* is a tall shrub of 1-2 metres in height, with longer racemes.

### **Gastrolobium appressum** C. A. Gardn. sp. nov.

Series *Racemosae* Benth.

Fruticulus 20-30 cm. altus, ramis subflexuosis, glabris, ramulis brevibus, dense foliolatis, appresse-pubescentibus, demum glabratis. Folia ternata, brevissime petiolata vel subsessilia, rigida, erecta, arcte appressa, coriacea, ovato-lanceolata, acuta, leviter concava, basi leviter sed conspicue rotundata, 6-7 mm. longa, manifeste reticulata, glabra, supra reticulata, subtus pallida; stipulae nullae. Flores ad ramulorum apices in racemulos pauciflorae, positae, pedicelli graciles, subpatentim sericeo-pubescenti, plerumque 2 mm. longi; calyx glaberrimus, 6 mm. longus, lobi 3 inferiores lanceolati acuminati.

tubum adaequantes; corolla calyce fere duplo longior, praeter carina purpurescenti, aurantiaco-lutea, alae carinaque vexillo breviores, aequilongae; ovarium villosum distincte stipitatum; legumen ignotum.

Hab. in distr. Irwin prope Gunyidi, in arenosis glareosis in fruticetis, fl. m. Septem. *Gardner* 12745 (TYPUS); prope Watheroo in locos similibus; in distr. Avon, Dalwallinu 25 km. occidentalem versus in arenosis saxosis.

The affinity is with G. *hamulosum* Meissn., but the branches are more divaricate, and the leaves appressed to the branchlets. The apparent complete absence of stipules is another feature distinguishing this species.

## MYRTACEAE

**Eucalyptus cupularis** C. A. Gardn. sp. nov.

Arbor usque 10 m. alta, cortice alba, basin versus rimosa, sursum leviter obtecta; ramulis leviter angulatis. Folia alterna, petiolata, rigida, crassiuscula, concoloria, opaca, in petiolum 2-2.5 cm. longum attenuata; lamina anguste lanceolata vel lanceolata, viridia, apici acuta vel acuminata, falcata, 16-18 cm. longa, costa media supra elevata et canaliculata, nervis lateralibus patentibus, anastomosis, nervus intramarginalibus ab margine distinctis.

Pedunculi axillari, erecti, validi, subtereti, sursum incrassati, 8-10 mm. longi, umbellam 5-7 floram gerentes; flores sessiles; alabastri juvenilibus bracteati.

Hypanthium cylindro-cupulatum, 5-6 mm. longum, laeve, basi contractum, 2-costatum vel -angulatum; 6 mm. longum; operculum late ovoideo-hemisphaericum, umbonatum, hypanthio brevior (3.5 mm. longum). Stamina adulta non visa, filamenta in alabastris flexuosis et incurva.

Fructus cylindrico-cupulatus, lignosus, diametro transversali 7-8 mm., sed tantum circa 8 mm. longus, margine crasso, discus elevatus, annulatus; capsula 4-5-locularis, valvis deltoideis, conspicue et rigide exsertis.

Hab. in distr. Ord, prope oppidum Hall's Creek, in colliculis lapidosis schistosis occidentalem versus *Gardner* 10217 (TYPUS) et in locis similibus *R. A. Perry* 3180; in montibus lapidosis in Lat. 18° 45′ S. Boundary Survey, *S. J. Stokes* sine n.

In the absence of flowers it is difficult to assign the systematic position of this attractive tree, and its affinities must remain obscure. It certainly has not been previously described.

**Euclayptus jucunda** C. A. Gardn. sp. nov.

Frutex elatus vel arbor parva, usque 7 m. alta, ramulis juvenilibus angulosis, brunneo-corticatis; folia alterna, distantia, viridiglaucescentia, oblongo vel anguste-lanceolata, falcata, in petiolum conspicuum circ. 1.2 cm. longum attenuatum, apice acuminata vel acuta, sine petiolo 6- usque 9 cm. longa, costa media prominula, nervis lateralibus supra vix conspicuis, subtus elevatis et conspicue obliqo divergentibus, laxe anastomosis, vena intramarginalia ab margine remota.

Pedunculi erecti, subtereti vel tantum obscure vel leviter angulosi, nunquam complanati, axillares sed plerique e ramulorum parti inferiorum foliorum jam destitutam enascentes, 1-1.2 cm. longi. Flores plerumque sat numerosos 6-12, manifeste pedicellatos gerentes; pedicelli subteretes, circ. 6 mm. longi, hypanthio vix breviores.

Hypanthium anguste-campanulatum, sub flore expanso circ. 6 mm. longum, basi attenuatum; stamina flavida, filamentis in alabastris flexuosa, inflexa, antherae oblongae, loculis parallelis; operculum late conicum vel ovoideum, acutum vel obtusum, 4 mm. longum.

Fructus ovoideo-globosus (diametro transversali 1.3 cm. metiens) sed tantum circ. 1.5-1.7 cm. longus, fere laevis ad marginem orifici 3.5 mm. diametro; capsula trilocularis, valvis profunde inclusis et apparenter tribus.

Hab. in distr. Irwin septentrionalem valde divulgatus in arenosis crescens; prope flumen Murchison in arenosis lutosis in fruticetis, *Gardner;* prope flumen Greenough juxta pontem mullewensem in fruticetis, fl. m. Febr. *R. D. Royce* 1122; prope Tenindewa, *G. H. Burvill;* haud procul a Yuna, *G. E. Brockway;* inter Mullewa et flumen Greenough, *J. Reeves* 70; in arenosis fruticetis prope flumen Greenough. fl. 6. Januario 1959, *Gardner* 12066 (TYPUS).

Belonging to the *Macrantherae,* this species does not appear to have any close affinities.

Blakely has named a variety *globosa* of *Eucalyptus eudesmioides* F. Muell. which I have not seen, but the species named here has no affinities with the *Eudesmieae.*

**Regelia megacephala** C. A. Gardn. sp. nov.

Fruticosum glabrum usque 3.5 m. altum, rami erecti, ramuli abbreviati, dense foliati. Folia opposita, quadrifariam decussata, erecta, vel leviter patentia, obovato-orbicularia, plana vel concava, sessilis, basi subcordata, glauco-viridia, subtus prominenter 5-nervia, breviter acuta vel mucronata.

Capitula globosa, ad ramorum valde abbreviatum terminantia, magna, rhachis albo sericeo-villosa; flores purpurae, pulchrae. Calycis tubus turbinatus, 2.5-3 mm. longus, albo-pubescens; sepala lanceolata, acuta, trinervia, calycis tubo longiores, villosa; petala alba subscariosa, fere oblonga, truncata erecta glabrique, marginibus hyalina, ciliata, circa 3.5 mm. longa; phalangium circ. 2-andrum, circ. 7 mm. longum, glabrum, antherae luteae.

Capitulae fructiferae ovoideo-globosae vel ovoideae, usque 3 cm. longae et 2.3 cm. latae. Calyces fructiferae plusminusve concretae, truncatae, late hemisphaerico-urceolatae, 1-1.2 cm. latae; calyx fructifer immersus late obovoideus, capsulam valde superans, valvis obtusis.

Hab. in distr. Avon prope oppidum Coomberdale, in collis saxosis quartzosis, fl. m. Decem. *Gardner* 12167 (TYPUS).

Affinity with *R. ciliata* Schau., differing principally in the glabrous branches, the erect and appressed obovate-orbicular larger leaves, the relatively longer calyx-lobes, and the much larger fruiting heads. The shrub is also much larger and erectly branched.

**R. velutina** (Turcz.) C. A. Gardn. comb. nov.

*Beaufortia velutina*, Turcz. in Bull. Phys. Math. Acad. Petersb. x, 346 (1852).

**R. cymbifolia** (Diels) C. A. Gardn. comb. nov.

*Beaufortia ? cymbifolia* Diels in Engler's Bot. Jahrb. xxxv. 431 (1904).

Diels did not see normal ♀ flowers of this plant. It proves to be a *Regelia*, and I have collected a topotype from the original locality:—prope Tambellup in fruticetis arenosis, fl. m. Oct. *Gardner* n. 13885.

### **Eremaea purpurea** C. A. Gardn. sp. nov.

Frutex rigidus circiter 30 cm. altus, ramis crassis, erectis densissime foliolatis, ramulis ultimis exceptis glaberrimus. Folia patentia, oblonga, crassa, supra concava, 2-2.5 mm. longa, obtusa, glaberrima, viridia, tantum leviter gladuloso-punctata. Flores purpurae, pulchrae, solitarii ad ramulorum apices sessiles, bracteis parvis, ovatis, caducis. Calycis tubus campanulato-turbinatus, argenteo-villosus, vix 3.5 mm. longus, lobi deltoidei subacuti, trinerves, tubo breviores glabri; petala purpurea, obovato-orbicularia, concava, obtusissima, erecta, glabra, circ. 4 mm. longa, marginibus subscariosa, basin versus attenuata; phalagium 15-andrum, filamenta purpurea, antherae flavae.

Calyx fructifer late hemisphaerico-cupulatus, capsula non superans, circ. 6 mm. longus. 9 mm. latus; semina erecta, inaequaliter tetragono-clavata, angulis membrana hyalina frimbriata alatis.

Hab. in distr. Darling prope Culalla, in arenosis humidis, fl. m. Decem. *Gardner* (TYPUS); prope Muchea in arenosis depressis, *H. Steedman*.

The affinity of this species is with *E. ebracteata* F. Muell., from which it differs in the much smaller and broader glabrous leaves, the small purple flowers and the relatively smaller calyx-lobes. The style is short and glabrous.

### **Melaleuca conothamnoides** C. A. Gardn. sp. nov.

§*Capitatae* Benth.

Frutex multiramosus circ. 1 m. altus, ramis erecto-patentibus, ramulis erectis, omnino glaberrimus; folia alterna vel sparsa, breviter petiolata, arcuato-patentia, oblongo-lanceolata vel oblonga, obtusa vel apicibus rigide mucronata, basi contracta vel breviter attenuata, glauca, rigida, plana vel leviter concava, 3-5-nervia. Capitula globosa vel ovoidea, ad ramorum partem superiorem terminantia, breviter pedunculata, rhachis breviter sericeo-tomentosa; flores mediocres, purpurae, calycis tubus late ovoideus, pubcrulus; calycis lobis breviter semiorbicularis, marginibus tenuiter hyalinis; petala ovata, purpurea, subscariosa, concava, obtusissima, patentia, glabra, marginibus integra; phalangium glabrum, purpureum circ. 13-andrum, antherae brevae, luteae. Ovarium triloculatum. Capitulae fructiferae globosae vel brevi-cylindricae vel ovoideae, 7-12 mm. longae et 9 mm. latae. Calyces fructiferae ovoideae, lobis deciduis; capsulam valde superans, cir. 4 mm. longae et 3 mm. latae.

Hab. in distr. Irwin inter Caron et Latham, *Blackall* 765; *Gardner* 2690; inter Morawa et Koorda, *Blackall* 3469 distr. Avon: Wongan Hills, *R. D. Royce* 2192; Ballidu, *Gardner*; prope Wyalkatchem, *J. W. Green* 835; *Blackall*; prope Tammin 5 km. occidentalem versus in arenosis glareosis in planietis, *Gardner* 1122, Novem. 1920 (TYPUS).

Austin distr. a form from Boolardy, collected by *A. B. Cashmore* has larger flower-heads and somewhat longer leaves.

The affinity of this species is with *M. cordata* Turcz., differing mainly in the shape of the leaves which are never cordate at the base, the almost petaloid calyx-lobes, and the more numerous filaments. Both species are often found in the same area under the same ecological conditions.

### **Leptospermum sericeum** Labill.

*Leptospermum sericeum* Labill. Nov. Holl. Pl. Sp. XI p. 9, pl. 147 (1806).

In September 1962, I collected at Cape Le Grand specimens of a *Leptospermum* in flower (Gardner 14117) which have been matched with the type in the Florence Herbarium.

Since 1867, when Bentham confused this species with *Kunzea sericea*, the species has been deleted from the Flora of Western Australia. Brown and Baxter both collected *Leptospermum sericeum* in fruit, and, since the specimens were not in flower, they were placed by Bentham under *Kunzea sericea*.

The recent collection of this attractive species proves that *L. sericeum* is the common plant of the islands of the Recherche Archipelago, since *Kunzea sericea* does not occur within 160 km. of the coast. Labillardiere's designation "Capite van Diemen" for the plant is due to an error.

### **Wehlia aurea** C. A. Gardn. sp. nov.

Frutex densus multiramosus, usque 40 cm. altus, omnino glaber; ramis erectis, virgatis, ramulis ultimis brevibus, denissime foliatis; folia confertissima, sparse, arcte imbricata, erecto-appressa, subsessilia, crassiuscula, elliptico-obovata, laevia, supra leviter concava, subtus convexa, crebre nigro-punctata, valde obtusa, 2 mm. longa.

Flores in ramorum apicibus denissime spicatae, brevissime pedicellatae, aureo-luteae, circiter 5-6 mm. diam.; bracteae scariosae, calycis tubus involventes, caducae, orbiculares, medio unicostatae, marginibus hyalinae. Calycis tubus hemisphaericus, vix 2 mm. longus, leviter compressus, lobi rotundati, tubo subaequalibus, glabri, marginibus scariosis, integri; petala orbicularia, aureo-lutea, marginibus integra. Stamina circ. 35-40; ovarium globosum; ovula 2. ad apicem placenta a basin collateraliter affixa; stylus elongatus.

Hab. in distr. Austin prope Pindar, in arenosis lutosis, fl. m. Oct. *Gardner* 7778 (TYPUS), etiam inter Perenjori et Dalwallinu *Blackall*, ad lacum Monger extendit; prope Canna in fruticetis arenosis, *Gardner* 2688.

The species is distinct in its minute appressed broadly obovate smooth leaves, in the whole plant quite glabrous, and in the leafy spikes of yellow flowers.

### **Wehlia grandiflora** C. A. Gardn. sp. nov.

Frutex 1.2 m. altus, ramis patentibus, omnino glabra. Folia petiolata, patentia, 5-6 mm. longa, cuneato-oblonga, subtriquetra, valde carinata, supra convexa, in apicem mucronatum recurva terminantia; flores purpurae, axillaribus solitarii vel bini, brevipedunculata; bracteae parvae: bracteolae scariosae, cordatae, arcte imbricatae; longitudinaliter striatae, purpureae, marginibus albis scariosis. Calycis tubus campanulatus, vel hemisphaericus, minute foveolato-punctatus; sepalis suborbicularibus, roseis, trinervis, lobis, hyalinis, petalis subdimidio. Petala roseo-purpurea, late obovata (apicibus subacuta), purpureo-striata; stamina numerosa (circi. 35-40) petala excedentia; filamentis purpureis; antherae oblongo-ellipticae, recurvae, rimis longitudinalier dehiscentibus, glandula cornuta, dorsalia, prominens, incurva; stylus flexuosus, compressus, staminibus longioribus, in depressis ovarii insertus; ovulis 2, collateraliter affixa

Hab. in distr. Austin prope Menzies 25 km. meridionalem versus, in arenosis dunosis, fl. m. Novem-Decem. *Gardner* 13879 (TYPUS).

Distinguished from all other species of the genus in the larger widely spreading longer leaves, the larger flowers and distinctly cordate bracteoles and long exserted style. Its closest affinity is *W. staminosa* F. Muell., which occurs on stony hills between Mount Hale, Meekatharra and Lake Carnegie.

### **Darwinia Masonii** C. A. Gardn. sp. nov.

§*Genetyilis* (D.C.) Benth.

Frutex erectus, 1.5-2 m. altus vel ultra, ramis erecto-patentibus, cortice albo-griseo. Folia dense conferta, basin versus attenuata et breviter petiolata, subtriquetra, pallide viridia, saepe 1 cm. longa, apice breviter acuta. Capitulis subsessilibus, ramulis terminantibus; involucrum hemisphaericum; bracteae numerossisimae, pluriseriatae, exteriores oblongo-lanceolatae interiores ovato-contractae, rubrae, usque 15 mm. longae; bracteolis oblongo-lanceolatis, valde concavis vel cymbiformis, submembranaceis, mucronulatis, 5 mm. longis. Calycis tubus circ. 4 mm. longus, durus, manifeste 10-costatus, inferiori turbinatus, lobis minutis; petala ovato-lanceolata, alba, circ. 3 mm. longa, obtusa, glabra; stamina 10, brevia, glabra; staminodia filamentis similia sed angustiora, aequilonga; stylus 10-11 mm. longus, sursum sparse et breviter pilosus, pilis patentibus.

Hab. in distr. Austin prope montem Gibson, in fruticetis in glareosis, fl. m. Aug. *D. Mason* (TYPUS).

This species is closely related to *D. leiostyla* (Turcz.) Domin, notwithstanding the totally different climatic and edaphic requirements. The involucral bracts are much like those of *D. leiostyla*, and in both species the calyx lobes are minute. The leaves however, are narrower and subtriquetrous, and the flower-heads smaller.

## VERBENACEAE

### **Lachnostachys bracteosa** C. A. Gardn. sp. nov.

Frutex nanus, circ. 20-30 cm. altus, ramis numerosis, erecto-patentibus, ramulis erectis. Folia opposita, decussata, linearia, sessilia et valde decurrentia, obtusa, supra glauca et ± transverse bullata, olivacea et sparse tomentosa, demum glabrescentia, usque 1 cm. longa, 1.5 mm. lata, marginibus arcte revoluta, subtus (costa media) albo-tomentosa.

Spicae terminales, cylindricae, dense albo-tomentosae, sessiles vel subsessiles; bracteae rigidae, lanceolatae, cymbiformae, petiolatae, solitariae vel tripliciter cum uno petiolo, marginibus longe tomentosae, dorso dense et longe brunneo-tomentosae, acutae, petiolae persistentibus. Calyx obovoideus, breviter pedicillatus, extra dense lanato-plumosus, sordide albus, lobis lanceolatis, acutis, tubus et lobis intus glabris. Corollae tubus turbinatus, calyce subaequilongus, tubo truncato pilis longibus intus prope basin ortis, exceptis glabro. Stamina 6-7 (rarius ad 2 reducta) filamenta elongata ad margine tubum affixa, dilute-violacea, basin versus dilatata; antheris dithecis, thecis rimis longitudinalibus dehiscentibus. Ovarium ovoideum vel globosum, dimidio superiore sericeo-pilosum; stigmato capitato.

Hab. in distr. Eyre prope lacum King occidentalem versus in fruticetis in arenoso-lutosis, fl. m. Oct. *Gardner* 13636 (TYPUS).

What appears to be a peculiarity in this species is to be seen in the cymbiform bracts which have a slender but rigid petiole. These are either single, or three-branched, each bract having a flower in its axil. These persistent petioles, simple or trifid, persist after the flowers have fallen, giving to the inflorescence a distinctive appearance not seen in any other species of *Lachnostachys*. The presence of the petioles of these bracts indicate that the inflorescence is not a spike, but a spike-like panicle. Whether or not this condition is found in other species (except *L. coolgardiensis* S. Moore, its closest affinity) remains to be seen. This, and the much-branched stems which are comparatively slender and more woody than in other species are another distinctive feature of the plant.

### **Newcastlia chrysophylla** C. A. Gardn. sp. nov.

Frutex circ. 4 m. altus, ramis erectis, dense tomentosis, ramulis erectis, aureo-tomentosis. Folia alterna, sparsa vel rare opposita, obovata usque late-obovata, petiolata, basin attenuata, cum petiola 14 mm.-3.7 cm. longa, 5 mm. ad 1.0 cm. lata, crassa, plana vel marginibus leviter recurva, supra medium crasse crenulato-dentata, obtusa, supra olivacea et scabrida, subtus dense aureo lanato-plumoso-tomentosa.

Spicae terminales 4-5 cm. longae paniculae dispositae, breviter pedunculatae, bracteae ignotae. Calyx globosus, 3-4 mm. longus, extus dense aureo-plumosus, lobis deltoideus, acutiusculis, intus glabris. Corollae tubus obovoideus, calyci subaequilongis, lobis late-oblongis, obtusis, albis, glabris; filamenta breviora, infra medium tubum adnata, superne libera, quam antherae multo longiora. Ovarium globosum, supra medium dense pilosum, 2-loculatum, loculis ? 1-ovulatis, ovulo unico tantum maturascenti; stylus brevissimus (2 mm. longus), sparse pilosus, breviter bilobus.

Crescit in distr. Austin flumen Murchison 40km. septentrionalem versus, in arenosis lutosis in fruticetis, fl. m. Decem. *Gardner* 12054 (TYPUS).

Only known from this locality, and apparently rare, this remarkable shrub is particularly attractive by reason of the dense golden tomentum of the undersurface of the leaves which contrasts with the dark olivaceous upper surface. The stem is often 7 cm. in diameter, and it is by far the largest species of this genus. The genus is found almost entirely on the desert regions of the continent, and its occurrence almost on the boundary of the South-West Province is remarkable. Its affinities are with *N. Dixonii* F. Muell. et Tate and *N. chrysotricha* F. Muell. differing from both in the leaves which are petiolate, and of different size and shape, having the golden calyces of *N. chrysotricha* which has linear leaves with revolute margins, and from *N. Dixonii* in the shape of the leaves and the spicate inflorescence.

The species is worthy of cultivation.

### **Pityrodia spectabilis** C. A. Gardn. sp. nov.

§*Eupityrodia* E. Pritzel

Suffrutex diffusus vel erectus, usque 15 cm. altus, sparse ramosus omnino dense lanatus, ramulis crassus, internodiis brevibus. Folia opposita, oblonga vel oblongo-obovata, sessiles, sed non decurrentes, plana, crassa sed mollis, marginibus integra, novellis dense lanata, vetulis sparsim floccosa, usque 5.3 cm. longa, obtusa, basi attenuata.

Flores numerosae in axillis superioribus dispositae, pedicellatae, magnae, pedicelli 3-4 mm. longi. Calyx fere ad basin divisus, 1.5 cm. longus, lobis lanceolato-obovatis, obtusis, dorso plumosis. Corolla coccinea vel aurantiaca, 3 cm. longa, ad basin tubi angusta, subito campanulato-dilatata, extus glabra, intus supra basin dense tomentoso-sericea, supra medium sparse et breviter pilosa; lobis brevibus, patentis, subaequalibus, semiorbicularis, obtusis, marginibus denticulatis. Stamina exserta, filamentis infra medium tubi insertis, antherae brevissime appendiculatae. Ovarium dense sericeo-pilosum; stylus glabrus, corolla excedens.

Hab. in distr. Irwin prope Buntine in arenosis lutosis, fl. m. Decem. *Gardner* 12023 (TYPUS); prope Canna, *D. H. Perry*, fl. m. Oct.

The species belongs to the Section *Eupityrodia* E. Pritzel with affinity to *P. axillaris* (Endl.) Druce differing in the much larger calyx and corolla—almost twice as long, the calyx-lobes being also much broader and thicker, the almost equal corolla-lobes which are denticulate and not entire, the much exserted stamens, and the dark or violet prominent striations of the corolla. It is by far the largest flowered member of the genus.

## LABIATAE

### **Prostanthera scutata** C. A. Gardn. sp. nov.

§*Euprostanthera*

Frutex nanus usque 20 cm. altus, ramosissimus, ramis erecto-patentibus, vel diffusis, crebro foliatus. Folia opposita, in petiolis abbreviatis attenuata, apice obtusa, basin versus attenuatus, mollis, plana, integra undique cano-tomentosa, uninervia, 8-15 mm. longa.

Flores in axillis superioribus dispositae, solitariae, breviter pedicellatae; bracteolae 2, lineari-spathulatae, 2.5 mm. longae. Calyx 1.2 cm. longus, venis reticulatis, labio supero aucto, late ovatus, breviter 3-lobatus; labio infero integro, superiore duplo breviore. Corolla pallide coerulea, extus undique breviter pilosa, intus glabra, circ. 15 mm. longa, tubo cylindrico supra ovarium leviter constricta, deinde ampliato, lobis suborbicularibus, obtusis, 2 superioribus obovatis alte connatis, inferioribus obovatis, lobo mediano emarginato, lateralibus ovato-oblongis, retusis, stamina inclusa, antheris omnibus appendiculatis. Calyx fructifer amplus, obtusus; labio supero magno 1.5-1.7 cm. longo, 1.5 cm. lato, rotundo, eleganter nervoso, breviter et obtuse 3-lobato; labio infero ovato, superius duplo breviore, obtuso.

Hab. in distr. Irwin prope flumen Hutt, in arenosis lutosis, fl. m. Decembri, *Gardner* 14266, (TYPUS) etiam prope oppidum Wilroy, in fruticetis in arenosis fl. m. Novem. *Gardner* s.n.

## GOODENIACEAE

### **Leschenaultia pulvinaris** C. A. Gardn. sp. nov.

§*Euleschenaultia* Benth.

Suffrutex humilis, dense ramosus ramis ramulisque prostratis, dense pulvinaris, usque 30 cm. diam.

Folia dense-conferta, rigida, lineari-subulata, apice longiuscule mucronata, dense and breviter hirsuta, 6-7 mm. longa et 0.4 mm. lata.

Flores in axillis superioribus solitarii; ovarium lineare strictum vel leviter curvatum, 5.5 mm. longum, glabrum, calycis-lobi subulati acuminati, 3.5-4 mm. longi, scabride-hispidissimi. Corolla coerulea, tubus circ. 6 mm. longus, extus glabrus, intus tota extensione sparse et breviter pilosus, lobi tubo subaequilongi, 2.3-3 mm. longi acuminati, omnes subaequaliter latiuscule alati, in flore patentes, alis latis, rotundis, obtusis, obsolete venosis; stamina 3.2 mm. longa, filamenta tenuia. Capsula ignota.

Hab. in distr. Stirling, a Corrigin circ 40km. meridionalem versus, in arenosis, fl. m. Oct. *Gardner* 13620 (TYPUS).

This species belongs to the Section *Euleschenaultia*, with affinity to *L. expansa* R. Br., from which is differs in the dense pulvinate habit, like that of *L. tubiflora* R. Br., and in the subulate hispid foliage and calyx lobes of which there is no counterpart within the genus.

It is known only from the type locality, and it may be in danger of extinction, the total area being less than half a mile in extent, and most of it farming land.

### **Goodenia sericostachya** C. A. Gardn. sp. nov.

§*Monochila* G. Don.

Herba biennis vel forsan perennis usque 35 cm. alta, dense albido-sericeo-tomentosa, caulibus teretibus, simplicibus vel plerumque erecto-ramosis, validis. Folia inferiora subrosulata numerosa, obovato-oblanceolata, basin versus sensim angustata, ima basis paulum dilatata, integra, usque 5 cm. longa et 12 mm. lata, obtusa, plana, crassa sed molliter tomentosa, folia caulina minora, circ. 2 cm. longa, obtusa, basi sessilia, integra.

Scapi elongati, robusti, paullum ramosi, dense villosi; flores sessiles dense conferti in spicam densam, inferne saepe interruptum, superne densiorum efformantes. Calycis tubus obovoideus, denissime sericeo-pilosus, calyci lobi oblongo-lanceolati, acuti, ovario subaequilongi. Corolla intense violacei, extus praeter alas glabra dense sericeo-villosa, lobi omnes subaequaliter alati; omnes subaequales digitatim patentes, acuti; stamina libera; stylus elongatus, breviter et sparse pilosus; indusium dorso breviter pilosum, margine breviter et dense ciliatum. Capsula ellipsoidea, 6 mm. longa, longe lanato-villosa, calycis lobis persistentibus coronata; semina nigra, subrotundata, tenuiter et anguste marginata.

Hab. in distr. Irwin circ. flumen Murchison 45 km. septentrionalem versus in arenoso-lutosis, fl. m. Decem. *Gardner* 12430, 5. Jan. 1960 (TYPUS).

This species is remarkable in that it combines the floral structure of *Goodenia* with the habit and inflorescence of *Verreauxia*. It must be included in the Section *Monochila*, with *G.*

*scapigera* R. Br. and G. *Watsonii* F. Muell. et Tate, but differs from these in the vestiture of the plant, and from all the species of *Goodenia* in the spicate inflorescence. It is a remarkably attractive plant. In the season of its discovery it was fairly common in the restricted area of its habitat, visits to the same area during the last two or three years have failed to disclose its presence, even when not in flower. It is probable, that like some other plants, especially *Velleia discophora*, it will not again appear until the country is burned.

The holotypes of the species described in this paper will be deposited in the Western Australian Herbarium.

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# Journal
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Volume 47 1964

Part 2

## Contents

6.—The Wooigorong Stony Meteorite. By G. J. H. McCall and P. M. Jeffery.

7.—The Agamid Lizards of the genus Tympanocryptis in Western Australia. By G. M. Storr.

8.—On Beryl from Western Australia. By P. L. C. Grubb.

9.—Contributiones Florae Australiae Occidentalis XIII. By C. A. Gardner.

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Vol. 47 Part 3

# 10.—Notes on the Skulls of two Western Australian Rodents with a key to the Skulls of the Rodents of Southwestern Australia

By Ernest Lundelius, Jr.*

*Manuscript received—18th February, 1964*

Remains of two species of Western Australian rodents, *Pseudomys (Gyomys) occidentalis* and *Pseudomys (Pseudomys) rawlinnae*, hitherto known from small samples and few localities have been found in several caves along the west coast of Australia and along the south edge of the Nullarbor Plain. *Pseudomys (Gyomys) occidentalis* is reported for the first time from the southern Nullarbor Plain. Minor morphological differences can be seen in samples from different areas.

*Pseudomys (Pseudomys) rawlinnae* is shown to vary in the presence of an accessory cusp on the anterior edge of $M^1$, the degree of interorbital constriction and the degree of development of the spine on the zygomatic plate. This variation makes it difficult to distinguish this species from *Pseudomys (Thetomys) nanus* on the basis of fragmentary material.

Statistical tables on each species and a key to the skulls of the rodents of southwestern Australia are given.

## Introduction

Investigations of cave sediments from Western Australia have resulted in the collection of abundant material of two species of rodents, *Pseudomys (Gyomys) occidentalis and Pseudomys (Pseudomys) rawlinnae*, which have previously been known only from sparse material.

The author (Lundelius 1957, 1960, 1963) has previously reported the presence of these two species in cave deposits in Western Australia but no details concerning their morphology were given. The samples which form the basis of this report are large enough to give reliable estimates of the variability of some cranial and dental characters. This should facilitate comparisons with samples from other areas as they are found.

The present samples are obtained from the following caves: Murraelellevan, 32° 2′S. 126° 4′E.; Madura, 32° 0′S. 127° 0′E.; Webb and Snake Pit, 31° 46′S. 127° 51′E.; and Abrakurrie, 31° 39′S. 128° 26′E.

## Pseudomys (Pseudomys) rawlinnae

This species was named by Troughton (1932) on the basis of material from the vicinity of Rawlinna, Western Australia. Finlayson (1939) described a series from the vicinity of Ooldea, South Australia and gave the range and mean of the measurements of four males and four females. All of the material considered here comes from caves along the Eyre Highway between Balladonia and Eucla.

The largest sample and the one which forms the basis of the statistical data, comes from Murraelellevan Cave. Smaller samples are available from Madura, Webb, Snake Pit and Abrakurrie caves. Except for the material from Madura and Abrakurrie caves which contain some fill, all the specimens were collected from the surface where they were associated with remains of the rabbit *Oryctolagus cuniculus* and the house mouse *Mus musculus*. These two species have been introduced by the European colonists within the last century. While there is always the possibility of the remains of the introduced species being mixed with older material, the condition and the thorough mixing of the bones indicates that all the surface material is essentially the same age. The presence of well-preserved bones of only small animals indicates that owls were responsible for the bone deposits.

The skull of this species closely resembles that of *Pseudomys shortridgei* but is smaller and more lightly built. The anterior edge of the zygomatic plate is gently concave as in *Pseudomys shortridgei*, but there is more of a tendency to develop a dorsal spine. Some specimens have a well developed spine, others have the dorsal border of the zygomatic plate angled but with no spine. Although members of the genus *Notomys* also have the spine they are easily distinguished by the broadening of the upper surface of the anterior part of the zygoma. There is no broadening in *Pseudomys rawlinnae*.

The skull shows considerable variation in the width and shape of the interorbital area (Fig. 1). The width of the zygomatic arches also appears to be variable but an objective measurement is difficult on the present material. Some of this variation in the skull is probably attributable to age differences. Two skulls (CNHM PM-4294, PM4352) which show narrow zygomatic width, shortened rostra and rounded skulls have unworn teeth indicating that they are from relatively young individuals. Sexual differences may also be involved but no data are available on sexual dimorphism.

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* Department of Geology, University of Texas, Austin, Texas.

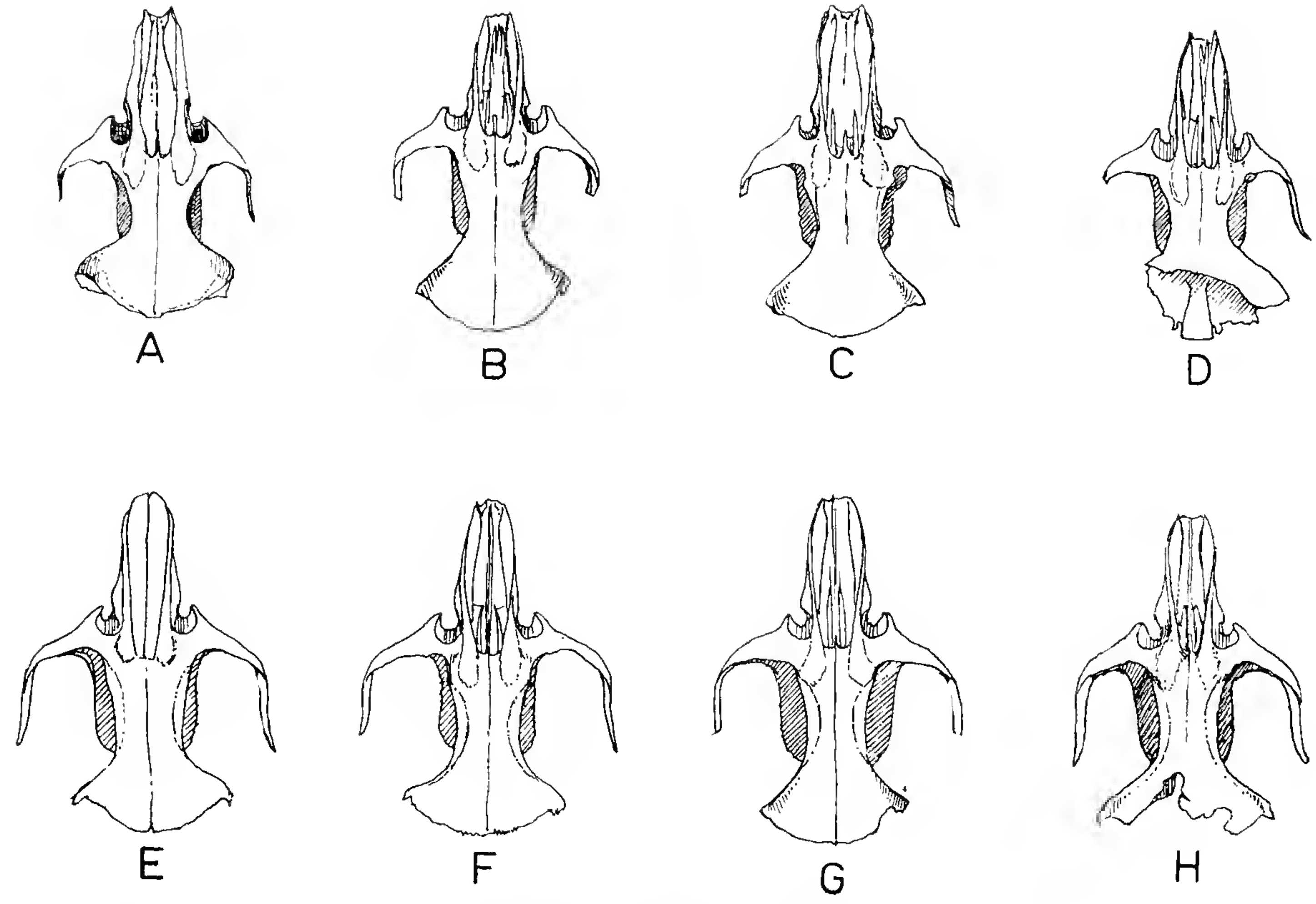

Fig. 1.—Dorsal views of eight skulls of *Pseudomys (Pseudomys) rawlinnae* from Murraelellevan Cave showing variation in interorbital region. x2. A—PM 4294; B—PM 4357; C—PM 4295; D—PM 4296; E—PM 4339; F—PM 4344; G—PM 4349; H—PM 4347.

**TABLE 1**

Statistical Data for a Sample of *Pseudomys (Pseudomys) rawlinnae* from Murraelellevan Cave and a Sample from Ooldea, South Australia.

| | Sample from Murraelellevan Cave | | | | | Sample from Ooldea* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | No. | Mean | Standard Deviation | Coefficient of Variation | Observed Range | 4 Males | | 4 Females | |
| | | | | | | Mean | Observed Range | Mean | Observed Range |
| Total length upper molars .... | 38 | 4·95 ± ·03 | ·23 | 4·6 | 4·64–5·48 | 5·1 | 5·0–5·2 | 5·2 | 5·0–5·3 |
| Length M$^1$ .... .... .... | 38 | 2·42 ± ·01 | ·097 | 4·0 | 2·23–2·65 | .... | ... | .... | .... |
| Length M$^2$ .... .... .... | 37 | 1·43 ± ·01 | ·11 | 7·4 | 1·30–1·76 | .... | ... | .... | .... |
| Length M$^3$ .... .... .... | 38 | 1·15 ± ·01 | ·084 | 7·4 | ·97–1·29 | .... | .... | .... | .... |
| Width M$^1$ .... .... .... | 38 | 1·66 ± ·01 | ·079 | 4·7 | 1·53–1·79 | .... | .... | .... | .... |
| Interorbital width .... .... | 22 | 3·88 ± ·04 | ·208 | 5·36 | 3·49–4·19 | 4·0 | 3·9–4·1 | 4·1 | 3·9–4·5 |
| Nasal length .... .... .... | 3 | 10·82 | .... | .... | 10·43–11·45 | 11·5 | 11·3–11·7 | 11·2 | 11·0–11·6 |
| Palatal length .... .... .... | 29 | 13·28 ± ·11 | ·608 | 4·58 | 12·21–14·55 | 15·6 | 15·1–16·3 | 16·0 | 15·6–16·6 |
| Length anterior palatal foramina | 29 | 6·17 ± ·09 | ·504 | 8·17 | 5·05–7·03 | 6·6 | 6·6–6·6 | 6·8 | 6·7–6·9 |
| Alveolar length upper molars .... | 39 | 5·40 ± ·04 | ·287 | 5·31 | 5·02–6·17 | .... | .... | .... | .... |

* Data from Finlayson (1939.)

The teeth are similar to those of *Pseudomys shortridgei* but, as in the case of the skull, they are smaller (Tables 1 and 2). The laminæ of the upper teeth do not slope as much as in *Pseudomys shortridgei.* The teeth show some variation in the degree of development of the external row of cusps, presence of an accessory cusp on the anterior edge of M$^1$ and the number of posterior cusps of M$^3$ and their configuration. Of 89 specimens from Murrælellevan Cave, 18 (or 20%) possess a well defined accessory cuspule on the anterior edge of M$^1$. A statistical comparison of samples with the cuspule and without it, shows no difference in the length of M$^1$. Of 79 right M$^3$'s from Murraelellevan Cave, 75 have a single posterior cusp free of the midloph, 2 have it connected to the midloph and 2 have two free posterior cusps.

## TABLE 2

*Statistical Data on a Sample of Pseudomys (Pseudomys) shortridgei from the Top One Foot of Sediments, Hasting's Cave, Western Australia.*

| | No. | Mean | Standard Deviation | Coefficient Variation | Observed Range |
|---|---|---|---|---|---|
| Total Length Upper Molars | 25 | 5·76 ± ·054 | ·27 | 4·70 | 5·23–6·11 |
| Length M¹ .... | 34 | 2·68 ± ·030 | ·18 | 6·54 | 2·32–2·91 |
| Length M² .... | 26 | 1·70 ± ·023 | ·12 | 6·99 | 1·45–1·91 |
| Length M³ .... | 25 | 1·35 ± ·021 | ·11 | 7·93 | 1·15–1·57 |
| Width M¹ .... | 34 | 1·91 ± ·018 | ·11 | 5·58 | 1·76–2·07 |

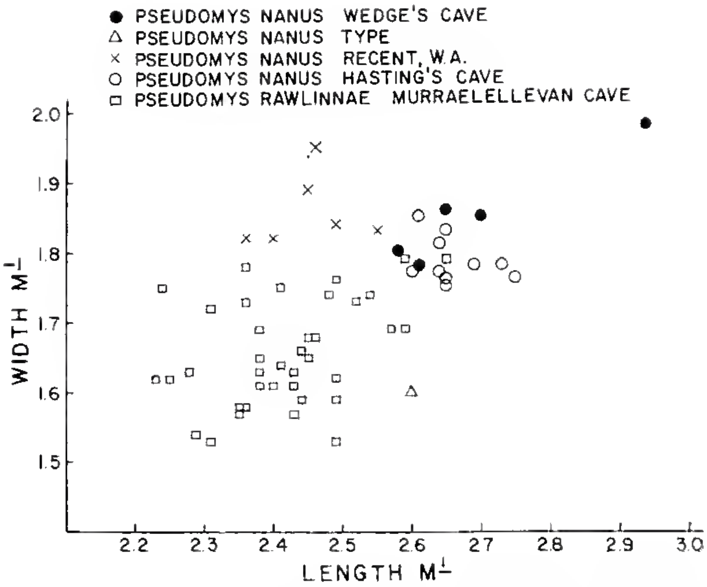

Fig. 2.—Scatter diagram showing relationship between length of M¹ and width of M¹ in several samples of *Pseudomys (Thetomys) nanus* and *Pseudomys (Pseudomys) rawlinnae* from Western Australia.

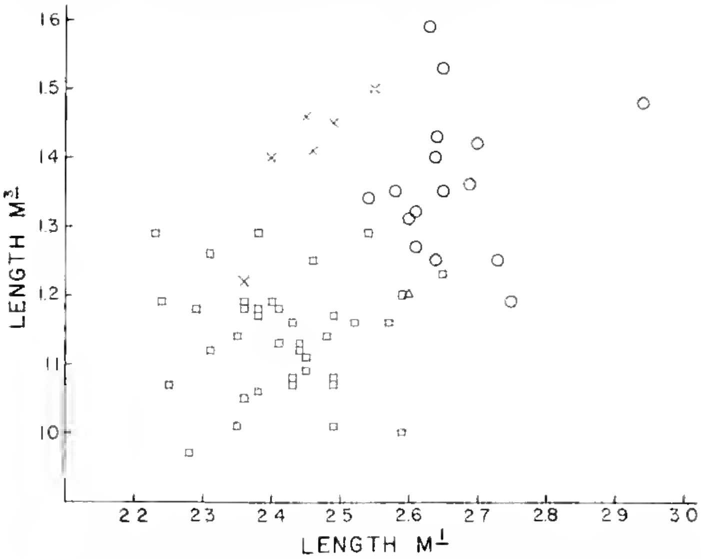

Fig. 3.—Scatter diagram showing relationship of length of M¹ and length of M³ in several samples of *Pseudomys (Thetomys) nanus* and *Pseudomys (Pseudomys) rawlinnae* from Western Australia. See figure 2 for explanation.

An examination of the coefficients of variation given in Table 1 reveals that they are all within the range to be expected in a population of mammals. This implies that either this population does not exhibit the high variability said to be characteristic of some Australian desert species (Jones 1923) or the sample from Murraelellevan Cave was accumulated in a very short period of time.

A comparison of the Murraelellevan Cave material with Finlayson's figures shows the two samples to be similar. However, a comparison of measurements of five characters of Finlayson's Ooldea sample with the Murraelellevan Cave sample shows that the former measurements always average larger. In two characters, nasal length and palatal length, no specimen from Murraelellevan Cave is as large as the largest Ooldea specimen (Table 1). These minor differences probably do not have much significance. Both samples are small so far as some characters are concerned and may not be representative of either population. It is to be expected that different populations of a species will show small differences.

The mandibles and lower dentitions are so similar to those of *Notomys mitchelli,* which occurs in the same area, that differentiation is extremely difficult and no attempt is made to describe them here.

The skull of *Pseudomys rawlinnae*, despite its general resemblance to that of *Pseudomys shortridgei*, is readily distinguished by its generally smaller size, lighter build and better developed anterior spine on the zygomatic plate. There seems to be no reason for not regarding them as good species until such time as morphologic intergrades are found.

*Pseudomys rawlinnae* is far more likely to be confused with *Pseudomys nanus*. Both species have a spine on the zygomatic plate, no broadening of the upper anterior surface of the zygoma and, as noted above, some specimens of *Pseudomys rawlinnae* have an accessory caspule on the anterior edge of M¹ as in *Pseudomys nanus*.

Figures 2, 3 are scatter diagrams of width of M¹ against length of M¹ and length of M¹ against length of M³ showing the relationships between a Recent sample of *Pseudomys nanus*, 2 subfossil samples of *Pseudomys nanus* and a sample of *Pseudomys rawlinnae.* It is clear that the principal difference between *Pseudomys nanus* and *Pseudomys rawlinnae*, is size. This is of little help in deciding whether they might be conspecific since size is frequently different in different populations of the same species. It is also interesting that the subfossil samples of *Pseudomys nanus* seem to show a slightly larger size than the Recent sample.

Although the type locality of *Pseudomys nanus* is along the west coast of Western Australia, a large part of the intervening area is essentially the same as the known area of occurrence of *Pseudomys rawlinnae* and it is quite possible that it actually occurs over a wide area. Finlayson (1941) has recorded a rodent which he refers to *Pseudomys nanus* from 10 miles south of Koonapandi in Central Australia. The presence of very similar rodents in widely scattered localities in central and western Australia suggests that they might be local populations of one widely distributed species.

### Pseudomys (Gyomys) occidentalis

*Pseudomys (Gyomys) occidentalis* was described by Tate (1951) from two specimens from Tambellup, southwestern Australia. Until the material from the caves in western Australia was discovered these were the only known specimens.

The material described here comes from caves along the west coast of Australia and from the Nullarbor Plain (Lundelius 1957, 1960, 1963). This new material not only adds to the known geographic range of the species but also shows that the species varies morphologically over its range.

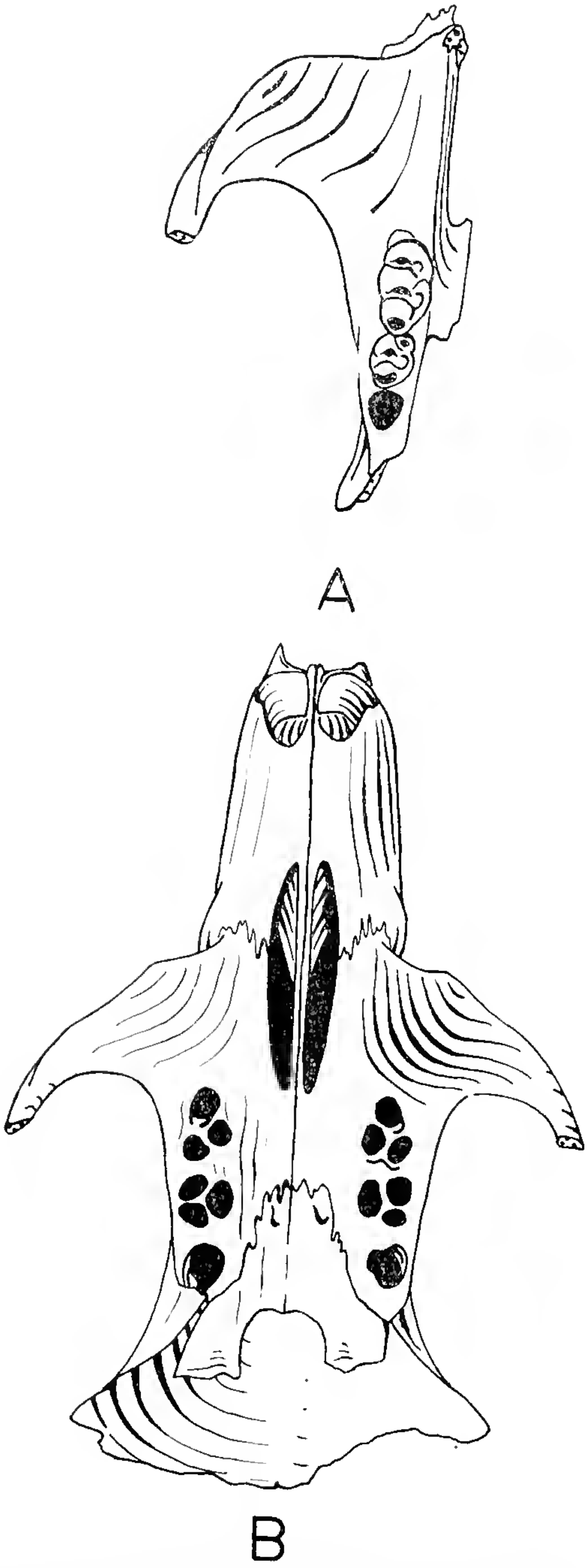

Fig. 4.—Ventral view of maxillary (A) and palate (B) of *Pseudomys (Gyomys) occidentalis* from Murraelellevan Cave, x 5.

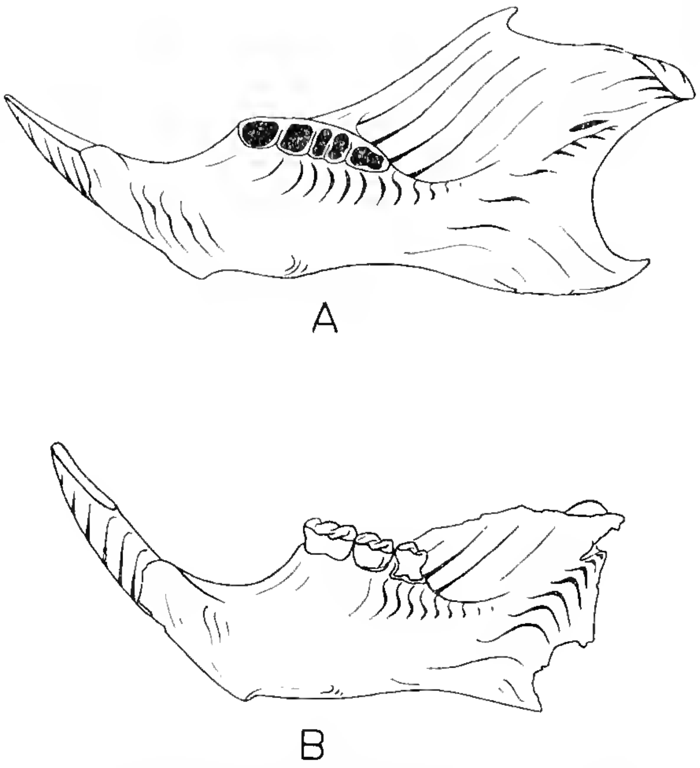

Fig. 5.—Lingual view of mandible of *Pseudomys (Gyomys) occidentalis* from Murraelellevan Cave, x 4.

The presence of *Pseudomys (Gyomys) occidentalis* in the Recent deposits at Jurien Bay reported by the author (Lundelius 1957) extended its known range 300 miles northward and indicated a wide distribution in the semi-arid portions of western Australia. The discovery of remains of this species in surficial deposits of Murraelellevan Cave on the Nullarbor Plains extends its range 500 miles eastward into a very dry area and indicates that the species had in the very recent past a very wide distribution in the southern part of western Australia.

The skull of this species is characterized by a broad zygomatic plate with a straight anterior edge and no spine at the top. The anterior part of the zygomatic arch is not broadened. The molars, both upper and lower, are very small in proportion to the size of the skull, very short crowned and have almost no inclination to the laminæ. No specimens have been seen with an accessory cuspule on the anterior edge of M$^1$.

Table 3 gives measurements for the type and paratype, several specimens from Murraelellevan Cave and statistical data on a sample from Hasting's Cave near Jurien Bay. It can be seen that there are few significant differences between these three widely separated samples. The greatest difference is the generally smaller size of the Nullarbor sample. Although the sample is small it consistently falls slightly below or in the lower end of the observed range of the Hasting's Cave sample.

The differences between the Hasting's Cave sample and the type and paratype from Tambellup are much smaller. The length of the lower molars, M$_1$, M$_2$, width of M$_1$, length of M$^1$, M$^2$ and width of M$^1$ of the Tambellup specimens are either slightly above or at the upper end of the observed range of the Hasting's Cave sample.

## TABLE 3

Statistical Data on a Sample of *Pseudomys (Gyomys) occidentalis* from the Surface Layer of Hasting's Cave and Murraelellevan Cave, Western Australia, compared with the Type and Paratype

| | Hasting's Cave Sample | | | | | Recent Western Australian | | Murraelellevan Cave Sample | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | No. | Mean | Standard Deviation | Coefficient Variation | Observed Range | CNHM 34725 Type | CNHM 34726 | No. | Mean | Observed Range |
| Length $M^1$ | 10 | 1·96 ± ·038 | ·12 | 6·28 | 1·78–2·14 | 2·09 | 2·11 | | | |
| Length $M^2$ | 15 | 1·36 ± ·01 | ·04 | 2·85 | 1·27–1·41 | 1·30 | 1·39 | | | |
| Length $M^3$ | 9 | 1·02 ± ·03 | ·09 | 8·70 | ·88–1·15 | ·95 | ·98 | | | |
| Width $M^1$ | 10 | 1·34 ± ·009 | ·03 | 2·24 | 1·28–1·44 | 1·37 | 1·47 | | | |
| Width across $M^1$'s (alveolar) | 12 | 5·20 ± ·052 | ·18 | 3·42 | 4·84–5·50 | | | | | |
| Width between $M^1$'s (alveolar) | 15 | 2·78 ± ·049 | ·19 | 6·82 | 2·22–2·99 | | | | | |
| Width across $M^3$'s (alveolar) | 5 | 5·11 | ·21 | 4·15 | 4·84–5·32 | | | | | |
| Width between $M^3$'s (alveolar) | 11 | 3·34 ± ·081 | ·27 | 8·02 | 2·92–3·80 | | | | | |
| Width across ant. end premaxilla | 16 | 2·75 ± ·065 | ·26 | 9·43 | 2·42–3·30 | 2·34 | 2·56 | | | |
| Upper alveolar length | 26 | 4·71 ± ·056 | ·29 | 6·19 | 4·26–5·82 | 4·44 | 4·46 | 2 | 4·30 | 4·26–4·34 |
| Length post incisor diastema | 21 | 7·66 ± ·091 | ·42 | 5·44 | 7·00–8·44 | 7·62 | 7·91 | | | |
| Interorbital width | 8 | 4·13 ± ·17 | ·50 | 12·19 | 3·68–5·23 | 4·04 | 4·32 | | | |
| Depth of rostrum at tubercle | 15 | 6·99 ± ·098 | ·38 | 5·43 | 6·08–7·45 | 6·18 | 6·57 | | | |
| Length incisive foramina | 16 | 4·96 ± ·065 | ·26 | 5·26 | 4·61–5·47 | 5·1* | 5·6* | | | |
| Length lower molars | 13 | 4·53 ± ·022 | ·08 | 1·78 | 4·38–4·68 | 4·58 | 4·67 | | | |
| Length $M_1$ | 20 | 2·01 ± ·013 | ·06 | 3·13 | 1·85–2·12 | 2·13 | 2·10 | 3 | 1·92 | 1·83–1·96 |
| Length $M_2$ | 14 | 1·35 ± ·008 | ·03 | 2·52 | 1·30–1·41 | 1·37 | 1·46 | | | |
| Length $M_3$ | 14 | 1·10 ± ·018 | ·07 | 6·72 | ·97–1·23 | ·99 | 1·07 | | | |
| Width $M_1$ | 20 | 1·19 ± ·009 | ·04 | 3·30 | 1·13–1·29 | 1·23 | 1·30 | 3 | 1·17 | 1·16–1·19 |
| Length lower post incisor diastema | 19 | 4·30 ± ·066 | ·29 | 6·65 | 3·73–4·91 | 3·82 | 4·10 | 4 | 3·93 | 3·56–4·19 |
| Alveolar length lower molars | 20 | 4·60 ± ·029 | ·13 | 2·80 | 4·39–4·86 | 4·62 | 4·58 | 4 | 4·54 | 4·15–5·42 |
| Depth of jaw at center $M_1$ | 18 | 4·12 ± ·059 | ·25 | 5·98 | 3·55–4·50 | 3·78 | 4·00 | 4 | 3·29 | 2·98–3·61 |

* Measurements from Tate (1951); CNHM, Chicago National History Museum.

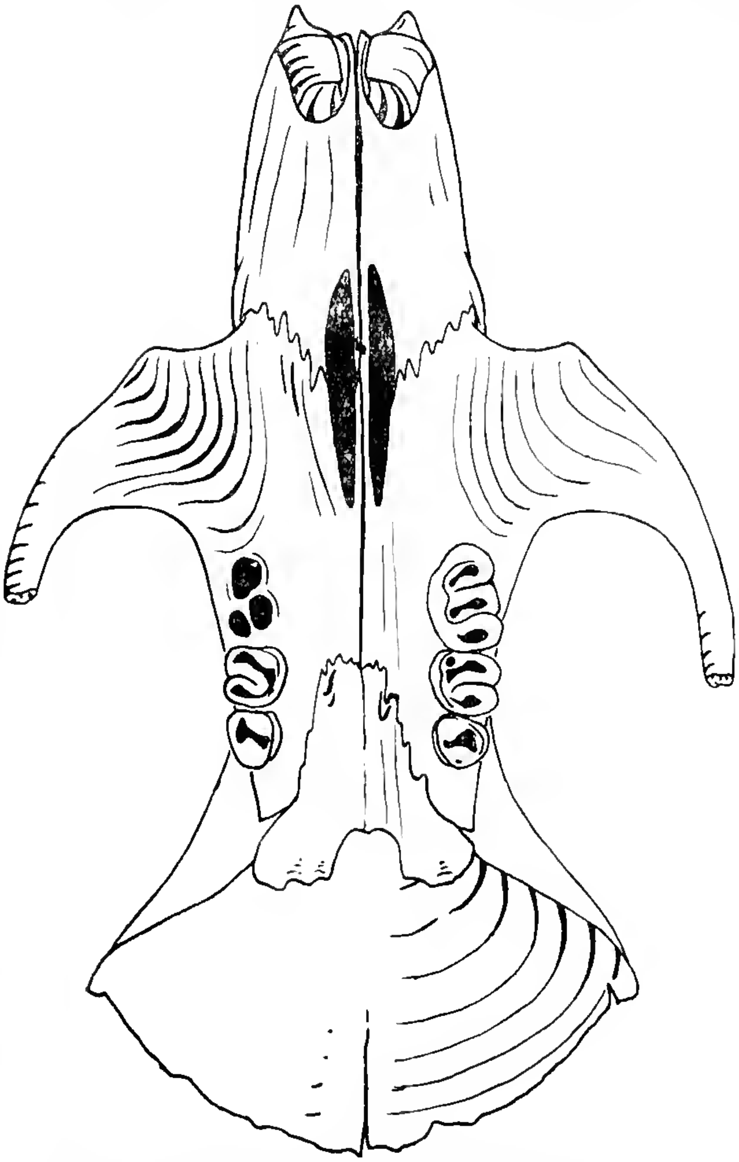

Fig. 6.—Ventral view of palate of *Pseudomys (Gyomys) occidentalis* (CNHM PM4233) from Hasting's Cave. x 5.

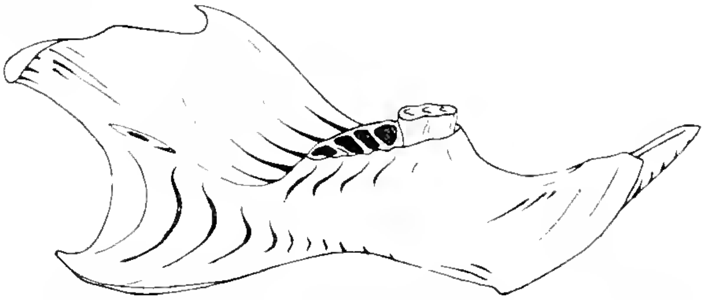

Fig. 7.—Lingual view of mandible of *Pseudomys (Gyomys) occidentalis* from Hasting's Cave. x 3.5.

These differences between samples would probably prove to be statistically significant if larger samples were available. The differences are of the kind and degree usually seen between subspecies and probably represent subspecies of *Pseudomys occidentalis.*

### Key to the Skulls of Rodents of Southwestern Australia

The identification of skeletal material of rodents is usually considered to be a task for a specialist with access to large collections of comparative material. This is frequently the case and will probably remain so in many instances. It is possible to find in the rodents of southwestern Australia consistent and easily recognized characters which, with few exceptions will allow an identification to species. The key presented here is based on the skull and upper teeth. The identification of the mandibles and lower teeth is very difficult even with access to comparative material.

The geographic area over which this key is expected to apply is western Australia from Geraldton to the south coast and eastward along the Nullarbor Plain to Eucla.

The identification of species of *Rattus* and *Mus* may give trouble. The recognition of the four species of *Rattus* mentioned in the key should give no trouble but additional species of *Rattus* may have been recently introduced from Asia and will not be identifiable. It is also probable that Asiatic species of *Mus* have been introduced recently. The author has seen specimens trapped in Western Australia which are not referable to any of the species of *Mus* or *Rattus* previously recognized in Western Australia.

A number of species of *Notomys* have been named from Western Australia, four from the western coastal area. Although Mack (1961) has synonomized many of these there is still no reliable way to differentiate the species on the basis of fragmentary material. Consequently this key does not go beyond the generic level.

Some characters, such as the presence of an accessory cusp on the anterior edge of $M^1$, the presence of a spine on the zygomatic plate and the number of roots on $M^1$, which are widely used in the literature should be used with some caution. The accessory cusp on $M^1$ is supposed to be present in *Pseudomys (Thetomys) nanus*, *Leggadina*, and present or absent in *Notomys* and absent in *Pseudomys (Pseudomys) shortridgei*. *Rattus* is supposed to have five roots on $M^1$; *Pseudomys*, *Leggadina*, *Notomys* are supposed to have three. The zygomatic plate is supposed to have a spine in *Pseudomys (Thetomys) nanus* and *Notomys*.

In fact, as noted above, a significant percentage of specimens of *Pseudomys (Pseudomys) rawlinnae* and a few specimens of *Pseudomys (Pseudomys) shortridgei* possess the anterior cuspule on $M^1$. The spine on the zygomatic plate is apparently always present in *Pseudomys (Thetomys) nanus* and *Notomys* and is variable in *Pseudomys (Pseudomys) rawlinnae*. A few specimens of *Pseudomys (Pseudomys) shortridgei* have four or five roots on $M^1$.

The result of these variations is the virtual impossibility of distinguishing positively *Pseudomys (Thetomys) nanus* and *Pseudomys (Pseudomys) rawlinnae* on the basis of cranial material. For this reason geographic distribution has been used to separate them until satisfactory morphological criteria are found.

A few specimens of *Pseudomys (Pseudomys) shortridgei* which have the anterior accessory cuspule on $M^1$ are unlikely to be confused with any other species because of size and the lack of a spine on the zygomatic plate. Those with more than three roots on $M^1$ are easily distinguished from *Rattus* by the poor development of the outer row of cusps on $M^{1-2}$.

| | | |
|---|---|---|
| 1. | $M^{3}_{3}$ absent; $M^{1}_{1}$ greatly enlarged (length greater than 6 mm), wears to form 3 large lakes; root pattern of $M^1$ complex | *Hydromys chrysogaster* |
| | $M^{3}_{3}$ present; $M^{1}_{1}$ not greatly enlarged | 2 |
| 2. | $M^1$ 5-rooted; 3 well developed cusps on 2 anterior lophs of $M^1$ | 3 |
| | $M^1$ 3-rooted (or occasionally 4), only 2 well developed cusps on 2 anterior lophs | 6 |
| 3. | Snout short; incisive foramina slit-like, occupying a large part of the post incisive diastema and extending well back of the front edge of $M^1$; interorbital constriction at middle of frontal | 4 |
| | Snout long; incisive foramina elliptical with rounded ends, occupying comparatively small part of the post incisive diastema and extending only to anterior edge of $M^1$; interorbital constriction well anterior to middle of frontal | 5 |
| 4. | Size large, molar row greater than 7 mm | *Rattus fuscipes* |
| | Size medium, molar row less than 7 mm | *Rattus sp.* |
| 5. | Zygomatic plate close to vertical; ridges on sides of braincase parallel | *Rattus norvegicus* |
| | Zygomatic plate inclined outward from skull; ridges on side of braincase rounded | *Rattus rattus* |
| 6. | $M^1$ longer than $M^2$ plus $M^3$ notch present on back side of upper incisors | *Mus musculus* |
| | $M^1$ shorter than $M^2$ plus $M^3$ notch absent on back side of upper incisors | 7 |
| 7. | Anterior edge of zygomatic plate concave with anterior projecting spine | 8 |
| | Anterior edge of zygomatic plate straight or convex | 10 |
| 8. | Anterior portion of zygomatic arch broadened (2 to 3 times wider than remainder of arch) | *Notomys* |
| | Anterior portion of zygomatic arch not broadened | 9 |
| 9. | Found in Nullarbor Plain | *Pseudomys (Pseudomys) rawlinnae* |
| | Found along west coast of Western Australia | *Pseudomys (Thetomys) nanus* |
| 10. | Size very small (length $M^{1-3}$ less than 4 mm) | 11 |
| | Size medium to large (length $M^{1-3}$ more than 4 mm) | 12 |
| 11. | Accessory cusp on anterior end of $M^1$ | *Leggadina hermannsbergensis* |
| | Accessory cusp not present on anterior end of $M^1$ | *Pseudomys (Gyomys) albocinereous* |
| 12. | Molars small in proportion to size of skull with weak laminae | *Pseudomys (Gyomys) occidentalis* |
| | Molars robust with well developed laminae and cusps | 13 |
| 13. | Size large (length $M^{1-3}$ more than 6.5 mm) with two rows of heavy cusps on upper molars | 14 |
| | Size medium (length $M^{1-3}$ less than 6.5 mm) with two rows of well developed cusps and one of poorly developed cusps on upper molars | *Pseudomys (Pseudomys) shortridgei* |
| 14. | Upper molar row more than 7.5 mm; a small oval foramen immediately behind upper incisors; bullae large | *Leporillus conditor* |
| | Upper molar row less than 7.5 mm; no small oval foramen immediately behind upper incisors; bullae small | *Leporillus apicalis* |

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# 11.—Effect of Salt, Temperature and Seed Scarification on Germination of Two Varieties of Arthrocnemum halocnemoides

By C. V. Malcolm*

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Green, but ripe seed heads of *Arthrocnemum halocnemoides* varieties *pterygosperma* and *pergranulatum* were collected and dried and the resulting seeds germinated well.

Germination of both varieties was tested in solutions containing nil, 0.8, 1.6 and 2.4 per cent sodium chloride. Tests were carried out in a factorial experiment at eight temperature regimes. Salinity caused reduction and delay in germination of both varieties. 50 per cent reduction in germination of *var. ptergosperma* occurred at about 8 g/l NaCl and of *var. pergranulatum* at about 20 g/l NaCl. Salinity and temperature interacted in their effects on germination.

*Var. pterygosperma* gave significant germination only at 5-35°C the temperature range at which *var. pergranulatum* gave best germination.

Scarified and unscarified seed of *var. pergranulatum* was tested at six temperature regimes. Scarification caused an increase and an acceleration of germination. There was an interaction between scarification and temperature.

## Introduction

Extensive areas of land in the agricultural areas of Western Australia are too highly saline for the growth of normal crops. As reported by Burvill (1956), in the results of a statistical survey, farmers in Western Australia estimated that in 1955 there were 933,000 acres of salty Samphire (*Arthrocnemum spp.*) flats or Ti-tree (*Melalenca spp.*) flats on their farms in the agricultural areas. This land is described by Smith (1961, 1961a) as "valley water-logged" and has an extremely salty watertable of 1,000 to 4,000 grains per gallon total soluble salts, closer to the surface than 4 ft.

Smith and Malcolm (1959) discussed the use of *Kochia brevifolia* and *Atriplex spp.* for growing on salt affected soils but the plants were not recommended for waterlogged areas. In seeking plants for waterlogged salty areas, the naturally occurring *Arthrocnemum spp.* have been investigated. The germination studies reported here are part of a programme of research into the use of *Arthrocnemum spp.* for sowing as fodder plants on highly saline winter waterlogged soils.

Seedheads of most plants dry off or ripen at some stage in their life cycle. The seed may then be harvested. In *A. bidens*, the seed heads are retained in a dried and woody condition. However, in *A. halocnemoides* varieties *pergranulation* and *pterygosperma* the seed heads, or inflorescences, may remain green and fleshy for several months after the seed has apparently ripened. As a result the opportunity for the inflorescences to dry off passes with the passing of summer. Green inflorescences were collected, air dried in the laboratory, and seed obtained by threshing and cleaning. The resulting seed germinated well and was used in the trials reported in this paper.

In some preliminary attempts at germinating seed of *Arthrocnemum spp.* in the laboratory it became clear that several factors were operative. Scarification appeared to assist germination of seed of *A. halocnemoides var. pergranulatum* and temperature seemed to influence germination of *var. pterygosperma.* The germination trials discussed in this paper were designed to elucidate these effects and to study the effects of salt, a factor of considerable importance in the natural habitat of the species.

## Method

### (i) Effect of temperature and salt on the germination of *A. halocnemoides* varieties *pergranulatum* and *pterygosperma*

The salinity treatments, nil, 0.8, 1.6 and 2.4 per cent. sodium chloride, were imposed by placing the seeds in 15 mls of the appropriate solution in a petri dish. The solutions were pipetted off and replaced at regular intervals to avoid concentration effects due to evaporation.

The temperature regimes were as follows:

| | | | |
|---|---|---|---|
| 20°C. | constant | 5-35°C. | fluctuating |
| 30°C. | ,, | 15-30°C. | ,, |
| 35°C. | ,, | 15-45°C. | ,, |
| 60°C. | ,, | 15-60°C. | ,, |

The fluctuating temperatures were thermostatically controlled to give gradual changes simulating normal day-night fluctuations as described by Quinlivan (1962).

The temperature and salinity treatments were combined factorially and three 50 seed replications were tested at each combination.

Germination was counted at 2-4 day intervals over the duration of the trial which lasted for 33 days. Germination was taken to have commenced when the radical emerged from the testa.

### (ii) Effect of Temperature and Scarification on Germination of *A. halocnemoides var. pergranulatum*

The following temperature regimes were used:

| | | | |
|---|---|---|---|
| 35°C. | constant | 5-35°C. | fluctuating |
| 60°C. | ,, | 15-30°C. | ,, |
| | | 15-45°C. | ,, |
| | | 15-60°C. | ,, |

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For each temperature three replications each of scarified and unscarified seed were tested. The scarification was applied at random to seedlots, after they had been counted, by lightly rubbing with fine emery paper.

Germination was counted at regular intervals over the duration of the trial which lasted for 28 days.

## Results

### (i) Effect of temperature and salt

Both temperature and salinity caused marked effects on germination (Table 1). *Var. pterygosperma* gave significant germination only in the 5-35°C. temperature treatment. *Var. pergranulatum* also showed a preference for the 5-35°C. range, but gave some germination at other temperatures.

A constant temperature of 60°C. gave rapid germination with *var. pergranulatum*, and seven days from the commencement of the trial the germination figures shown had been reached. No germination occurred thereafter. It appeared that the high temperature had broken the dormancy of the seed but caused a high mortality rate. By contrast seed in the 5-35°C. range did not commence to germinate until seven days had passed but reached a final percentage of 75 as against 36 per cent. for the 60°C. treatment.

There was an interaction between temperature and salinity effects similar to that shown by Malcolm (1963) for *Kochia brevifolia*. While 0.8 per cent. NaCl caused no reduction in germination of *var. pergranulatum* at 5-35°C., at 60°C. it caused a reduction from 36 to 25 per cent. germination. Similarly, 1.6 per cent. NaCl caused a reduction from 75 to 52 per cent. (31 per cent reduction) in germination of *var. pergranulatum* at 5-35°C., but at 60°C. a reduction of from 36 to 13 per cent. (64 per cent. reduction) was caused. Thus, in each case salinity and a temperature of 60°C. interacted to give greater reductions in germination than was shown for either factor operating separately.

**TABLE 1**

*Effect of temperature and salt on germination of two varieties of Arthrocnemum halocnemoides*

(mean per cent. germination from 3 replications of 50 seeds)

| Variety | pterygosperma | | | | pergranulatum | | | |
|---|---|---|---|---|---|---|---|---|
| Salinity | 0 | 0·8 | 1·6 | 2·4 | 0 | 0·8 | 1·6 | 2·4 |
| Germination 14 days after commencement of experiment | | | | | | | | |
| Temperature °C. : | | | | | | | | |
| 20 | 1 | 1 | 0 | 0 | 0·3 | 0 | 0 | 0 |
| 30 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 35 | 1 | 1 | 0 | 1 | 7 | 3 | 3 | 1 |
| 60 | 0 | 1 | 0 | 0 | 36 | 18 | 11 | 0 |
| 5-35 | 7 | 4 | 0 | 1 | 28 | 17 | 3 | 0 |
| 15-30 | 3 | 1 | 0 | 0 | 4 | 3 | 1 | 0 |
| 15-45 | 1 | 1 | 0 | 0 | 6 | 1 | 1 | 0 |
| 15-60 | 1 | 1 | 0 | 0 | 10 | 6 | 1 | 1 |
| Final Germination 33 days after commencement of experiment | | | | | | | | |
| Temperature °C. : | | | | | | | | |
| 20 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 0 |
| 30 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 35 | 1 | 1 | 0 | 1 | 8 | 4 | 3 | 1 |
| 60 | 0 | 1 | 0 | 0 | 36 | 25 | 13 | 3 |
| 5-35 | 72 | 37 | 15 | 2 | 75 | 75 | 52 | 0 |
| 15-30 | 4 | 1 | 0 | 0 | 4 | 5 | 5 | 0 |
| 15-45 | 1 | 1 | 1 | 0 | 10 | 3 | 1 | 0 |
| 15-60 | 1 | 1 | 0 | 0 | 20 | 13 | 1 | 1 |

Three temperature factors appear to influence germination. As discussed, high temperature accelerates germination of *var. pergranulatum*, though similar effects were not noted for *var. pterygosperma*. The effect of high temperature is shown in the germination of *var. pergranulatum* in the progressive increase in germination through the 15-30°C., 15-45°C., and 15-60°C. ranges. High temperature failed to affect germination of *var. pterygosperma*.

A second factor operating is temperature fluctuation, the effect of which is most clearly seen in the results for *var. pterygosperma*. While constant temperatures of 20, 30 and 35°C. gave almost no germination, a fluctuating temperature of 5-35°C. gave 72 per cent. germination.

Finally a relatively cold temperature is required by both varieties as the minimum temperature in the fluctuating range. Ranges of 15-30, 15-45, and 15-60°C. gave almost no germination with *var. pterygosperma* but a range of 5-35°C. gave high germination. The range 15-45 C. is of the same magnitude, 30 degrees, as the 5-35°C. range but does not include a sufficiently cold temperature. *Var. pergranulatum* gave similar results but effects of high temperature caused a variation. It is of interest to note that germination of both varieties occurred in the glasshouse where the temperature range was approximately 10-31°C.

The specific temperature requirements indicate dormancy problems. The response to the 60°C. treatment suggests hard-coatedness (see below). The response to fluctuating temperatures and to a relatively cold temperature e.g. 5 or 10°C. may be due in part to hard-coatedness and partly to physiological dormancy.

### (ii) Effect of Temperature and Scarification

In this trial, the effects of temperature were similar to those discussed under Section (i), but varied in the effect of high temperature. 60°C. constant and 15-60°C. fluctuating temperatures failed to give comparable figures. The reason for this is not known but may have been due to the use of a different batch of seed.

Scarification caused a marked increase and acceleration in germination. For the 5-35°C. range unscarified seed gave a germination of 43 per cent., but scarified seed gave 64 per cent. germination. In the 15-45°C. range the difference was even greater, 11 per cent. germination being obtained without scarification and 46 per cent. with scarified seed.

Scarification resulted in reasonable germination being obtained at temperatures which normally gave very poor results. For example 35°C. germination without scarification was 9 per cent. but with scarification was 36 per cent.

Seed which had been scarified gave 34 per cent. germination by the end of 13 days testing at 15-45°C. but unscarified seed had only given 5 per cent. germination over this period. The large difference was due in part, to the accelerating effect of scarification.

It is likely the scarification treatment was not even on all seeds in view of the difficulty of scarifying such tiny seeds in a controlled manner. The seeds are encased in a hard black testa and scarification was continued until the

## TABLE 2

Effect of temperature and scarification on germination of *A. halocnemoides* var. *pergranulatum* (mean per cent. germination from 3 replications of 50 seeds each)
(commenced 11.x.63)

| Date | Scarified |  |  |  |  |  | Unscarified |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Temp. °C. |  |  |  |  |  | Temp. °C. |  |  |  |  |  |
|  | 35 | 60 | 5–35 | 15–30 | 15–45 | 15–60 | 35 | 60 | 5–35 | 15–30 | 15–45 | 15–60 |
| 14.x.63 | 0 | 0 | 0 | 1 | 3 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16.x.63 | 5 | 3 | 0 | 2 | 10 | 9 | 0 | 1 | 0 | 1 | 2 | 1 |
| 17.x.63 | 7 | 3 | 1 | 2 | 17 | 10 | 0 | 1 | 2 | 1 | 3 | 1 |
| 21.x.63 | 9 | 3 | 16 | 7 | 25 | 11 | 2 | 1 | 3 | 1 | 3 | 2 |
| 24.x.63 | 12 | 4 | 23 | 9 | 34 | 12 | 3 | 1 | 4 | 3 | 5 | 3 |
| 28.x.63 | 33 | 5 | 32 | 11 | 39 | 13 | 5 | 1 | 13 | 5 | 7 | 4 |
| 31.x.63 | 36 | 11 | 55 | 16 | 45 | 15 | 9 | 4 | 39 | 7 | 10 | 5 |
| 6.xi.63 | 36 | 11 | 64 | 17 | 46 | 17 | 9 | 5 | 43 | 7 | 11 | 6 |
| 8.xi.63 | 36 | 11 | 64 | 17 | 46 | 17 | 9 | 5 | 43 | 7 | 11 | 6 |

majority of seeds in the sample bore light coloured patches. The variations are accounted for in the design of the experiment.

### Discussion

(i) Effect of temperature and salt

Novikoff (1946) reported 50 per cent. reduction in germination for several vegetable crops to occur at 18-22 gm/l NaCl. Malcolm (1963) found that for *Kochia brevifolia* 50 per cent. reduction in germination occurred at 15-20 gm/l NaCl. In the present study, *var. pterygosperma* gave 50 per cent. reduction in germination at about 8 gm/l NaCl, and *var. pergranulatum* probably at about 20 gm/l NaCl. It may be concluded that from the point of view of salt tolerance at germination, *var. pergranulatum* is similar to many vegetable crops and *var pterygosperma* is less tolerant.

The results indicate that temperature is a vital factor determining when *A. halocnemoides* will germinate. Moreover, germination will not occur when the salinity of the soil solution is greater than 2.4 per cent. NaCl. Smith (1961a) reported seasonal changes in salinity of a bare soil at Quairading. *Arthrocnemum spp.* are growing nearby. The lowest value obtained for the 0-¼ inch samples was 0.80 per cent. NaCl on the oven dry basis in July and the average for the July sampling was 1.11 per cent. NaCl. The soil in question was a fine sandy clay loam. The combination of low winter temperatures and high salinity would provide a severe limitation to the germination of the varieties under study. It is apparent that the plants have developed a means of avoiding germination into too harsh an environment. A great deal of rain would be required to leach salts from the topsoil sufficiently to allow germination to occur.

The results indicate that field planting of the species could be undertaken in the autumn before rain makes the soil unworkable, and the seeds would germinate when conditions become favourable. Salt tolerance of the seedlings must increase extremely rapidly and early in life surpass that of most other plants.

(ii) Effect of Temperature and Scarification

The scarification treatment was more effective in breaking dormancy than the best temperature regime under test, but still did not ensure good germination at unfavourable temperatures. On the other hand the seed coat appears to be slowly permeable on at least a proportion of seeds—those which germinate at 5-35°C. without scarification. Scarification allows the slowly permeable seeds to germinate more rapidly and allows further impermeable seeds to germinate.

Assuming the main effect of scarification is to allow water to gain ready access to the seed, an interaction can be shown between scarification and temperature. Germination of scarified seed can be considered as the potential germination for each temperature range. Leaving seed unscarified would be expected to cause the same proportional decrease in germination at all temperatures. However, at 15-45°C. the germination of unscarified seed amounted to 11 per cent, about one quarter that for scarified seed. Whereas at 5-35°C. unscarified seed gave 43 per cent. germination, about two thirds that for scarified seed. The 5-35°C. temperature range appears to influence the permeability of the seed coat in some way and make up for non-scarification.

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# 12.—Ashbed and Nutrients in the Growth of Seedlings of Karri (Eucalyptus diversicolor F.v.M.)

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When karri seedlings were grown in pots of soils from karri forest areas they showed remarkable responses to nitrogen and phosphorus fertilizers. The addition of nitrogen or phosphorous fertilizers separately gave only small increases in yield of seedlings, while the simultaneous addition of both fertilizers gave very large responses (up to three-fold in height and twenty-fold in dry weight).

Responses to ash and to heat treatment of the soil were also obtained. The major part of the ash response was shown to be due to the supply of phosphorus in the ash. The heat response is also believed to be largely due to increased supply of nutrients.

It is suggested that part of the well known ashbed response of karri forests is due to nutrients released in the ashing process

## Introduction

Growth of karri (*Eucalyptus diversicolor* F.v.M.) seedlings in the south-west of Western Australia is stimulated considerably in ashbeds where heaps of forest slash have been burned (Loneragan, 1961). Growth of young karri seedlings in non-ashbed areas is generally so poor that deliberate creation of ashbeds has become part of karri forest regeneration practice.

Karri ash contains plant nutrients including phosphorus, calcium, magnesium, and potassium (Stoate, 1950; Hatch, 1960) which may be important in the ashbed response. However, other marked chemical and physical changes are associated with ashbed treatment (Hatch, 1960) and no nutrient responses of karri have been recorded.

The work described in this paper was undertaken to assess nutrient deficiencies of a number of karri soils for optimum growth of karri seedlings, and to see to what extent nutrients might account for some of the stimulating effects of ashbeds.

## Methods

### Experiments 1, 2, 3.

General.—A red-brown sandy loam (karri-type) soil was taken from an area which showed typical ashbed response in regenerating karri seedlings at Crowea, 20 miles south of Manjimup. Soil from the top six inches was sieved, mixed, and 3,000 g placed in plastic bags in unglazed earthenware containers of 8-inch diameter at the surface.

All fertilizer additions are expressed as weight/acre calculated from a surface area basis (1 cwt/acre = 0.405g/pot). The plastic bags were perforated so that the soil was freely drained. The pots of soil were kept in the open at the Forests Department, Manjimup.

Karri (*Eucalyptus diversicolor*) seeds were sown in all pots on August 11 and 12, 1961. Natural rain was supplemented by de-ionised water as required. Plants were thinned to 5 per pot on October 2, to 3 per pot on October 30, and to 1 per pot on December 6.

The heights of plants from cotyledonary node to growing point was measured at frequent intervals throughout the experiment; data in tables refer to heights on April 26, about two weeks prior to harvest. At this time the thickness of the stem just above the cotyledonary node was also measured with calipers.

Shoots and roots of plants of experiments 1 and 3 were separated at the cotyledonary nodes and harvested on May 4 and 3, 1962, respectively; plants of experiment 2 were not harvested.

Harvested material was dried in an oven at 105°C, cooled in a desiccator, and weighed.

Detail.—*Experiment 1*—To test the effects of nutrients on the ashbed response of karri seedlings on karri-type soil.

No basal fertilizers were applied. Treatments were applied in quadruplicate, in a 2 x 2 x 2 factorial design as follows:

Heat—nil or 12 hours at about 150°C in an oven; the soil was placed directly in the earthenware pot for this purpose; the plastic bag was replaced after treatment.

Ash—nil or 3 tons of ash/acre. Ash was collected from tree bark which had been burned in a hot fire; it was mixed throughout the top inch of soil.

Nutrients—nil or N, P, K, Ca, Mg, Mn, Cu, Cl, Zn, B, Mo, Co. The nutrients were added as the same salts, at the same rates, and in the same manner as were used for basal and for treatment dressings in experiment 2, with the omission of $NaH_2PO_4$.

*Experiment 2*—to test the response of karri seedlings on karri-type soil to applications of K, Ca, Mg, S, Mn, Cu, Cl, Zn, B, Mo, and Co fertilizers.

Basal dressings of nitrogen and phosphorus were applied. $NH_4NO_3$ was applied at 14 cwt/acre in aliquots of 1 cwt/acre to the soil surface at regular intervals. Phosphate was applied as either the sodium or the potassium salt at levels equivalent in phosphate to 4 cwt of superphosphate/acre.

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Treatments were applied in an unreplicated $2^5$ factorial design as follows:

$KH_2PO_4$ at 1.5 cwt/acre or $NaH_2PO_4$ at 1.3 cwt/acre
$CaCO_3$ — nil or 2 cwt/acre
$MgSO_4$ — nil or 56 lb/acre
$MnSO_4.4H_2O + CuSO_4.5H_2O + ZnSO_4.7H_2O$ — nil or 14 + 7 + 7 lb/acre
$Na_2B_4O_7.10H_2O + (NH_4)_6.Mo_7O_{24}.4H_2O + CoCl_2.6H_2O$ — nil or 3½ + 1 + 1 lb/acre.

All salts except $CaCO_3$, which was applied in solid form, were applied in solution to the surface of the soil. When all salts had been applied they were mixed through the surface inch of soil.

*Experiment 3*—To test the response of karri seedlings on karri-type soil to applications of N, P, and K fertilizers.

Basal dressings of salts of Ca, Mg, S, Mn, Cu, Cl, Zn, B, Mo, and Co were applied. The nutrients were applied as salts in the same form, rate, and manner as the nutrient treatment in experiment 2, with the omission of $KH_2PO_4$ and $NaH_2PO_4$.

Two treatments were applied in octuplicate in a 2 x 2 factorial design as follows:

$KH_2PO_4$ — nil or 1.5 cwt/acre applied in solution to the soil surface.
$NH_4NO_3$ — nil or 14 cwt/acre applied as in experiment 2.

### Experiment 4.

Loamy sand was taken from the surface of soils in two adjacent areas on either side of a narrow jarrah-marri (*Eucalyptus marginata-E. calophylla*) and karri-marri ecotone at Snake Gully near Manjimup (see Plate 1, Loneragan, 1961).

The soils were prepared at the same time and in the same way as the karri soil used in experiments 1, 2, and 3, with the exception that six-inch diameter pots were used. (0.23 g of fertilizer/pot 1 cwt/acre).

A simple experiment was designed to test the effects of nitrogen and phosphorus fertilizers on the growth of karri seedlings on the karri-marri and the jarrah-marri soils.

The basal and treatment dressings of fertilizers were identical to those of experiment 3. The treatments were imposed in duplicate.

### Experiment 5.

Loam was taken from ashbed and non-ashbed areas of the surface soil of a regenerating karri forest at Easter Brook, 20 miles west of Manjimup. Pots of soil were prepared as in experiment 4.

Treatments consisted of either no fertilizers or dressings equivalent to 10 cwt of commercial N, P, K mixed fertilizer ("Nitrophoska red") per acre. These were imposed in duplicate.

Seed was sown on 11 July, 1962, thinned to 1 plant per pot, and harvested on 15 may, 1963.

### Experiment 6.

Loam was taken from ashbed and non-ashbed areas of the surface soil of a regenerating karri forest at Mattaband, 35 miles south-east of Manjimup. Pots of soil were prepared as in experiment 4.

Treatments were applied in duplicate as follows:

N — nil or 10 cwt of calcium ammonium nitrate/acre.
P — nil or 10 cwt of lime-super/acre.

Karri seeds were sown on 1 June, 1962, thinned to 1 plant per pot, and harvested on 15 May, 1963.

### Experiments 7, 8.

General.—Soil was taken from the same area as in experiments 1, 2, and 3. Soil from the top six inches was mixed and 1,800 g placed in plastic bags in polystyrene containers of 6-inch diameter at the surface (0.23g fertilizer/pot = 1 cwt/acre). The containers were not drained and the water content of the soil was maintained around field capacity by adding deionised water to weight. The plants were grown in a glasshouse at Perth: the glasshouse was shaded to about half natural daylight from December 1.

Karri seeds were sown in all pots on August 8, 1962. Plants were thinned to 5 per pot on September 11, and to 1 per pot on November 16. Tops of plants were harvested on December 19, 1962 and treated as in experiments 1, 2, and 3.

Detail.—*Experiment 7*—To test if some of the response of karri seedlings to ash is due to supply of phosphate.

Basal dressings were applied of salts of N, K, Mg, S, Mn, Cu, Zn, B, Mo, and Co. N was applied in solution as $NH_4NO_3$ in aliquots of 1 cwt/acre given at intervals throughout the experiment to give a total of 4 cwt/acre. All other basal nutrients were applied in the same form and at the same rate as in experiment 3; in addition, $K_2SO_4$ was applied in solution at 2 cwt/acre. The basal dressings were pipetted on the soil surface, allowed to dry, and mixed thoroughly with all the soil in the pot.

Treatments were applied in quadruplicate in a 4 x 4 factorial design as follows:

P — phosphate equivalent to superphosphate at 0, 4, 10, or 25 cwt/acre: the replicates were split into pairs which received either $KH_2PO_4$ or $NaH_2PO_4$ in solution at appropriate rates.
Ash — 0, 1, 3, or 9 tons/acre: ash was prepared as in experiment 1.

After application, the treatments were allowed to dry and were mixed thoroughly through the volume of the soil.

*Experiment 8*—To test if the response of karri seedling to ash is due in any way to an effect on nitrogen supply.

Basal dressings were applied of salts of P, K, Mg, S, Mn, Cu, Cl, Zn, B, Mo, and Co. The salts were applied in the same forms and at the same rates as in experiment 2, with the omission of $NaH_2PO_4$ and $CaCO_3$, and the inclusion of $K_2SO_4$ at 2 cwt/acre. The basal dressings were pipetted on the soil surface, allowed to dry, and mixed thoroughly with all the soil in the pot.

Treatments were applied in quadruplicate in a 2 x 2 factorial design as follows:

$NH_4NO_3$ — nil or 4 cwt/acre applied in solution in aliquots of 1 cwt/acre.
Ash — nil or 3 tons/acre: ash was prepared and mixed as in experiment 4.

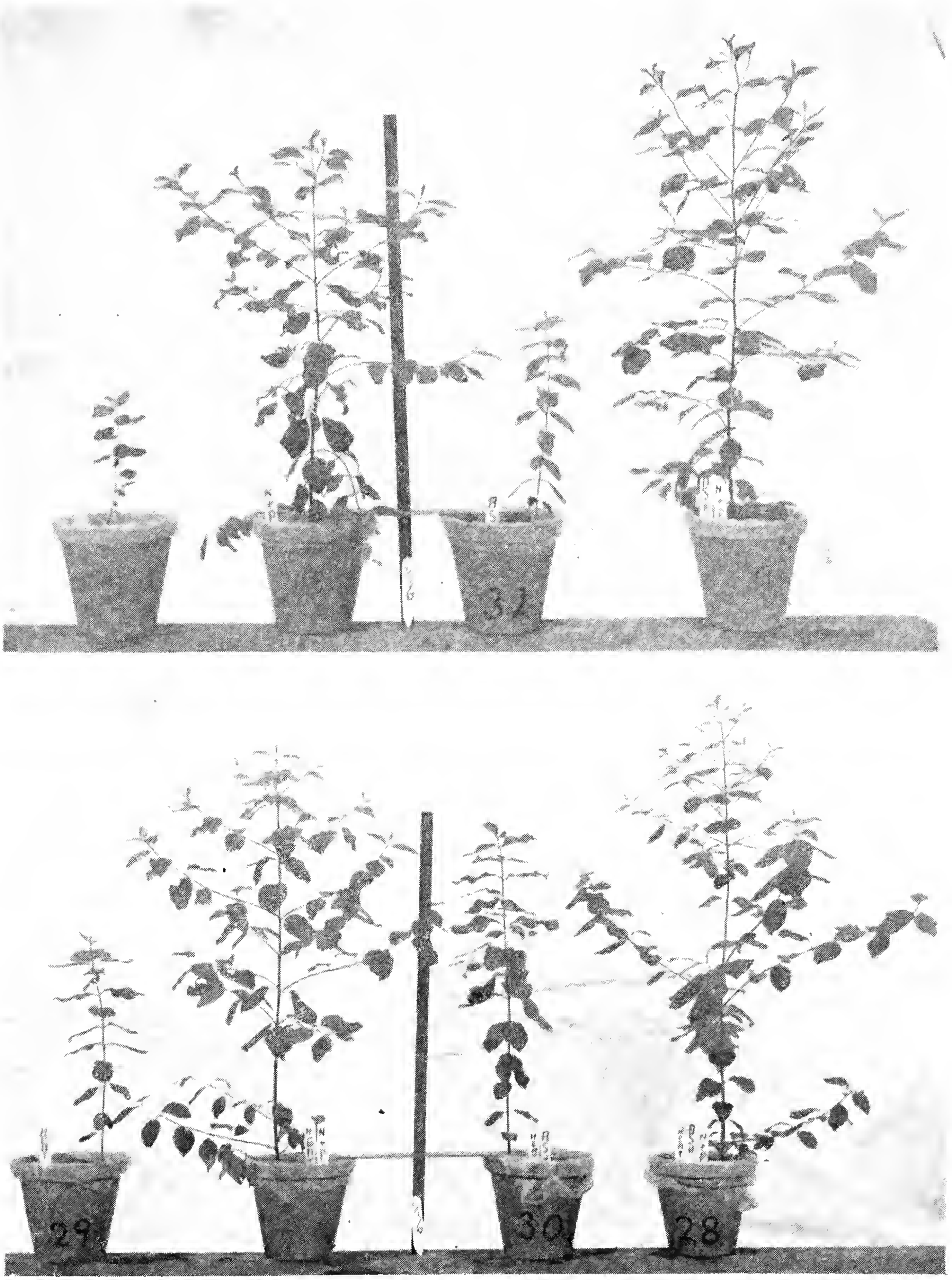

Fig. 1. Effects of ash, heat, and nutrients on the growth and form of karri seedlings grown for eight months in pots of karri topsoil (Experiment 1). Top—no heat. Bottom—heat treatment of soil before planting. Left to right—no ash, no nutrients; no ash, + nutrients; + ash, no nutrients; + ash, + nutrients.

## Results

### *Ash, heat, and nutrient responses*

Ashbed treatments markedly stimulated the growth of karri seedlings grown in pots of karri soil (Table 1). Application of ash, in the absence of nutrients and of heat treatments, increased the height of the seedlings one-and-a-half times, doubled the stem diameter, and trebled the dry matter of tops and roots. Heat treatment of the soil prior to sowing also gave, in the absence of ash and of nutrients, similar large increases in seedling growth.

**TABLE 1**

*Effects of ash, heat, and nutrients on the growth of karri seedlings for eight months in pots of karri topsoil (Experiment 1).*

| | Nutrients | No Heat | | Heat | |
|---|---|---|---|---|---|
| | | −Ash | +Ash | −Ash | +Ash |
| Dry weight of shoot ($g \times 10^{-1}$ per plant) | — | 7 | 26 | 35 | 79 |
| | + | 162 | 271 | 259 | 353 |
| Height of shoot—cm. | — | 27 | 41 | 45 | 59 |
| | | 66 | 83 | 76 | 87 |
| Diameter of stem—cm. x $10^{-2}$ | | 14 | 26 | 24 | 37 |
| | | 52 | 57 | 60 | 65 |
| Dry weight of shoot—percentage maximum | — | 2 | 7 | 10 | 23 |
| | + | 46 | 77 | 73 | 100 |
| Height x girth—percentage maximum | — | 1 | 7 | 7 | 22 |
| | | 48 | 73 | 74 | 100 |

All main treatment effects, significant at $P < 0{\cdot}001$: all interactions, not significant. Dry weight data were transformed to square roots before analysis.

Nutrients applied to the same soil stimulated karri seedling growth to an even greater extent than ashbed treatments (Table 1). In the absence of ash and heat treatments, nutrients nearly trebled height growth and stem diameter and increased dry matter production twenty-fold. The more striking stimulation of dry matter production, compared with height and stem diameter, was partly due to the effects of nutrients in increasing branching and leaf production (Fig. 1) and partly due to the fact that the weight of the main stem increases with a function of the product of its height and square of its diameter. Despite the striking effects of treatments on seedling form, the product of height x girth reflected relative effects of treatment on dry weight production very closely (Table 1).

In the presence of ash and heat treatments, nutrients again increased growth of karri seedlings. Interactions between treatments were in all cases not significant.

### *The nature of the nutrient response*

The striking effect of the nutrient mixture in stimulating karri seedling growth was due almost entirely to the supply of nitrogen and phosphate in the mixture. None of the nutrients K, Ca, Cu, Mn, Zn, Co, Cl, B, or Mo, was deficient in the soil since, when nitrogen and phosphate were applied, the omission of any of them had no effect at all on the appearance, shoot height, or stem diameter of karri seedlings. The omission of $MgSO_4$ from the nutrient mixture had no effect on shoot height, but depressed stem diameter slightly (by 13%: significant at 5%). No dry weight data were collected on plants of this experiment. On the other hand, the failure to supply either nitrogen or phosphorus to the seedlings, even in the presence of all other nutrient salts, led to severe restriction of growth (Fig. 2).

For optimum seedling growth, nitrogen and phosphorus appear to be deficient in many karri forest soils. Large responses of karri seedlings were obtained when nitrogen and phosphorus fertilizers were applied to pots of all soils examined (Table 2).

**TABLE 2**

*Effects of nitrogen (N) and phosphorus (P) fertilizers on the growth of karri seedlings grown in pots of various soils from karri forest areas (Experiments 4, 5, 6)*

Dry weight of shoots ($g \times 10^{-1}$ per plant)

| | −N −P | −N +P | +N −P | +N +P |
|---|---|---|---|---|
| Snake Gully (karri-marri) | 8 | 16 | 17 | 96 |
| Snake Gully (jarrah-marri) | 2 | 4 | 4 | 109 |
| Easter Brook (ashbed) | 20 | .... | .... | 77 |
| Easter Brook (non-ashbed) | 21 | .... | .... | 76 |
| Mattaband (ashbed) | 11 | .... | .... | 86 |
| Mattaband (non-ashbed) | 4 | 14 | 21 | 91 |

### *The nature of the ash response*

Phosphorus.—A major part of the effect of ash in stimulating karri growth on soil in pots was due to an increase in phosphorus supply to the plant (Table 3). As in previous experiments, karri seedlings grew poorly when phosphorus was omitted from the soil to which all other known essential nutrients were added. In the absence of phosphorus, addition of ash up to 9 tons per acre increased dry matter production of the shoots six times. But in the presence of phosphorus the response to ash disappeared (interaction significant at $P<0.001$).

**TABLE 3.**

*Effects and interactions of phosphate fertilizers and ash on the growth of karri seedlings grown for four months in pots of karri topsoil given adequate dressings of other nutrients (Experiment 7).*

Dry weight of shoots ($g \times 10^{-1}$ per plant).

| Ash Tons/acre | Form of Phosphate | Phosphate (= P in cwts super/acre) | | | |
|---|---|---|---|---|---|
| | | 0 | 4 | 10 | 25 |
| 0 | Na | 4 | 67 | 69 | 76 |
| | K | 4 | 66 | 70 | 50 |
| 1 | Na | 8 | 69 | 66 | 74 |
| | K | 7 | 71 | 77 | 77 |
| 3 | Na | 12 | 72 | 72 | 81 |
| | K | 13 | 77 | 79 | 84 |
| 9 | Na | 18 | 73 | 82 | 77 |
| | K | 28 | 70 | 84 | 75 |

The response of karri seedlings to ash in this experiment is thus due to its effect on phosphorus supply. This effect is explained by the phosphorus actually added to the severely phosphorus-deficient soil in the ash (0.3%). A dressing of 9 tons of ash per acre would contain

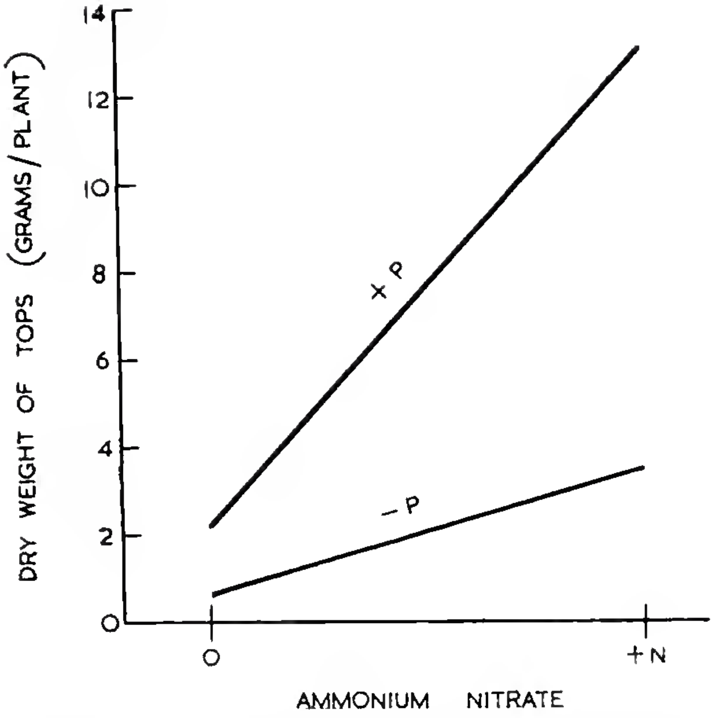

Fig. 2.—Effect of ammonium nitrate (N) and potassium phosphate (P) on the growth of karri seedlings grown in pots of karri topsoil given adequate levels of other nutrients (Experiment 3). Interaction significant at $P < 0.001$.

phosphorus equivalent to 6 cwt of superphosphate per acre. The failure of this treatment to stimulate growth of karri to the same extent as equivalent dressings of phosphate salts was probably due to poorer availability of the phosphorus from the ash.

Nitrogen.—In addition to increasing phosphorus supply to karri seedlings, ash treatment increased nitrogen supply to an appreciable extent (Table 4). In the presence of all known nutrients except nitrogen, karri seedling growth was again poor. In the absence of nitrogen, addition of ash doubled the yield of shoots. In the presence of nitrogen there was no response at all to ash (interaction significant at $P < 0.001$). Thus, in this experiment the response to ash must have been due entirely to an effect in increasing nitrogen supply.

**TABLE 4**

*Effects and interaction of ammonium nitrate and ash on the growth of karri seedlings grown for four months in pots of karri topsoil given adequate dressings of other nutrients. (Experiment 8).*

Dry weight of shoots (g x $10^{-1}$ per plant)

| | — Ash | + Ash |
|---|---|---|
| No ammonium nitrate .... .... .... | 8 | 19 |
| + ammonium nitrate .... .... .... | 86 | 86 |

The ash contained no measurable nitrogen, so that its effect on nitrogen supply must have been indirect.

Other factors.—Although in experiments 7 and 8 all of the ash response was replaced by nutrients, in experiment 1 there was some response to ash even in the presence of nutrients. The additional response given by ash in the presence of nutrients was probably partly due to the supply of sub-optimal amounts of nitrogen in the nutrient treatment, combined with heavy leaching in the early stages of growth. However, it is still possible that in experiment 1 a small part of the ash response in the presence of nutrients was due to factors other than nitrogen and phosphorus supply. Because of small differences in experimental technique (e.g. size and drainage of the pots, depth of mixing of treatments, water supply), it is not possible to make an absolute comparison between experiment 1 and experiments 7 and 8.

However, it is clear that under all conditions, nitrogen and phosphorus supply are the major limiting factors to the growth of karri seedlings on the soils examined. It is also clear that the prime effect of ash is to increase the supply of phosphorus.

## Discussion

A number of soils from karri forests have been shown to be extremely deficient in both nitrogen and phosphorus for the growth of karri seedlings. Soils from regenerating *Eucalyptus obliqua* forests have previously been shown to be deficient in phosphorus for growth of *E. obliqua* seedlings (Attiwill, 1962). It seems, then, that the growth of seedlings and perhaps also of trees regenerating in eucalypt forests may be limited by the same widespread deficiencies of nitrogen and phosphorus which limit the growth of agronomic crops on so many Australian soils.

Beadle (1954, 1962) has in fact suggested that soil phosphorus status is an important determinant of plant communities in *Eucalypt* forest areas of eastern Australia. In addition, he has shown a marked response of the seedlings of three *Eucalypt* species to soils with increasing phosphorus status. His photographs show changes in leaf size and seedling form with increasing soil phosphorus similar to those produced by nutrients in karri seedlings.

The striking nutrient responses of karri seedlings reported in this paper should not be extrapolated directly to the forest. The results were obtained with seedlings grown for a very short period of time, in the absence of competition, and with adequate water. All of these conditions are modified in the forest. Moreover, nutrient treatments in pots caused dramatic changes towards a different form of the karri seedlings. However, the results do indicate the potential which exists for stimulation of tree growth by adding fertilizers to karri forest soils.

Heat treatment of soils and dressings of wood ash also stimulated growth of karri seedlings. The effects of ash were shown to be largely due to increased phsophorus supply to the seedlings. Heat treatment of forest soil has also been shown to liberate phosporus for the growth of *Eucalyptus obliqua* seedlings (Attiwill, 1962). In addition, heat treatment of the same soil appears to have released some nitrogen to the seedlings. There are reports of increased supply of nitrogen from organic matter after heating (Vlamis *et al.*, 1955), although there may, in fact, be a loss of total nitrogen from the soil through burning (Barnette and Hester, 1930). It is suggested that in the present experiment the main effects of heat may also have been through the release of nutrients for the growth of karri seedlings. No attempt was made in this work to resolve the effects of heat.

Even when the soil had been heat treated and large quantities of ash applied, nutrients stimulated karri seedling growth. This suggests that ashbed responses in the forest could be greatly augmented by fertilizers. Such fertilizers would probably be best applied at the earliest opportunity to encourage trees to dominate the site.

In some pot experiments, nutrients replaced ash. However, the effects of fire which produce ashbeds in the forests are complex (see review by Ahlgren and Ahlgren, 1960). Therefore, extrapolation to the forest situation of the effects of heat and ash treatments on the growth of karri seedlings in pots has even more limitations than the extrapolation of nutrient responses. Marked effects of burning forest slash on the physical and chemical properties of the soils in karri forests have been recorded by Hatch (1960). In addition to these effects, burning of forest slash may modify the viability of seed and therefore the regeneration of plants in the vicinity. Heat from the fire may destroy surface roots and seeds of competitive species, and so permits unhindered germination and growth of seed freshly introduced from above by seed trees in the area. This competition-free seed bed may be an important part of the ashbed response in karri regeneration (Loneragan, 1961). At the same time, the ability of seeds of some *Acacia* species to germinate is increased by mild heat conditions on the fringe of the ashbed, so that leguminous species may be favoured to colonize the fringe areas of the ashbed. In the long term, these species could be expected to improve the nitrogen status of the soil. Such changes in the botanical composition of the competitive species produced by ashbeds could produce marked changes in the competition which the karri suffers for light, nutrients, and water.

Whatever the complexity of the long term ashbed response, the results presented in this paper clearly indicate that nutrients supplied by ashbeds could make an important contribution to the accelerated growth of young karri seedlings in the ashbeds of regenerating forests.

## Acknowledgements

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# 13.—Foraminiferal Evidence for the Paleocene Age of the King's Park Shale (Perth Basin, Western Australia)

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Several species of foraminifera in the King's Park Shale are found also in other Australian faunas dated firmly as Paleocene. Some, including *Globorotalia chapmani* Parr, *Globorotalia pseudomenardii* Bolli, *Lamarckina rugulosa* Plummer, are Paleocene index fossils. There is no significant evidence for dating the King's Park Shale as Eocene.

## Introduction

In 1938 the late W. J. Parr described a foraminiferal fauna found in samples from two bores in King's Park, Perth, Western Australia. Parr concluded that the fauna was Eocene, and probably Upper Eocene, in age. Later he prepared several more samples, mainly from the nearby Langley Park bore, which were richer in both numbers and age-diagnostic species than the original material. However, nothing further had been published on the fauna when Parr died in 1949. The fauna has been studied subsequently but no worker has made a serious attempt to revise Parr's conclusions in the light of new, richer material or the recent major advances in our knowledge of Lower Tertiary biostratigraphy. Nevertheless this assemblage and its dating have been relied upon quite heavily, particularly by Crespin (see refs.), in studies of other Lower Tertiary faunas in Australia.

The material prepared by Parr has been used by the writer for comparative purposes in his studies on the Australian Paleocene (unpubl. thesis, 1962). This paper presents evidence for redating the King's Park Shale as Paleocene. Reference is made continually to the Paleocene faunas of the Carnarvon Basin, Western Australia, and the Otway Basin, Victoria. Papers in preparation on these faunas will discuss and figure most of the species invoked here, as well as some of the repercussions in species identification arising from the age revision of the King's Park Shale. However, *Globorotalia chapmani* Parr is discussed and figured below.

*Material.*—King's Park Bore No. 1: 10 samples between 780 ft. and 120 ft.

King's Park Bore No. 2: 8 samples between 728 ft. and 150 ft.

Langley Park Bore: 7 samples between 975 ft. and 208 ft.

Claremont Bore: 1 sample, 300-350 ft.

Types of 17 species erected by Parr and other specimens.

Specimens separated by M. F. Glaessner from core at 1505 ft., South Perth Bore (see Glaessner 1956).

For localities, see Coleman, 1952, text-fig. 1.

## Acknowledgements

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## Stratigraphic Relationships

The following notes are based on McWhae *et al.* (1958) and references given by these authors.

The sedimentary sequence under consideration, part of the thick infill of the Perth Basin, has been named the King's Park Shale by Fairbridge (in Coleman, 1952). The formation is known only from bores in the Perth area, where it varies, in drilled thickness, from 660 feet in the King's Park no. 1 bore to more than 1000 feet in the South Perth bore, less than two miles away. The sequence consists of grey calcareous shales and mudstones, pyritic in part. The King's Park Shale overlies the South Perth Formation (uppermost Jurassic to Lower Aptian) and the Osborne Formation (?Aptian, Albian to Cenomanian); and it is succeeded by Quaternary limestones and clays.

## Previous Studies

In arriving at his conclusions, Parr (1938, p. 69, 90) relied largely on Cushman's studies on the North American Eocene and Oligocene faunas. Cushman published on the Paleocene of North America largely between 1940 and 1949; also, important studies on Paleocene faunas by Brotzen (1948) and others were not available to Parr. Added to these points in Parr's defence are several others: the Midway of Texas (Plummer 1927) was thought of as Lower Eocene instead of Dano-Paleocene; the biostratigraphic value of planktonics was becoming appreciated only then (e.g., Glaessner 1937a); and the Upper Eocene microfaunas of southern Australia were not yet known. Indeed, very little has been published on the Paleocene even to the present day. Consequently it is hardly surprising that Parr's conclusions can be revised by new approaches to the problem.

Concerning the King's Park fauna, Crespin (1950, p. 424) stated that " . . . there is no indication with what part of the Eocene it can be correlated". Subsequently, however (Crespin

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1954, 1956a,b, 1958, Raggatt and Crespin 1955). Crespin has emphasized the similarity of various faunas mostly in South Australia and Victoria to the fauna described by Parr; and she has accepted the Upper Eocene age of the latter. On the other hand, Crespin (1956a) has noted the similarity in some respects of the King's Park fauna to the Paleocene faunas of the Carnarvon Basin (see also below).

Coleman (1952) studied the foraminifera from six bores in the Perth metropolitan area. He noted (p. 37) that "the faunal assemblage as a whole is unlike that of any other region in Australia"; but he did not discuss its age, concentrating instead on bore-to-bore correlation. In a footnote (p. 42), however, Coleman records a suggestion by Crespin that the King's Park assemblages are closely similar to the faunas in the Swedish Paleocene (Brotzen 1948), and that "it is probable then that at least part of the fauna of the Perth Basin . . . is of Paleocene age". Glaessner (1956) and Belford (unpublished report to Bureau Mineral Resources, Canberra; referred to by Cookson and Eisenack, 1961) found King's Park Shale species in samples from the South Perth and Rottnest Island bores respectively. Both workers dated their samples on the basis of Parr's conclusions.

Churchill (1960) refers in passing to the Paleocene age of the King's Park Shale at a relatively high level in the subsurface (Narrows bore 164 ft.). Churchill's evidence presumably is palynological but to the writer's knowledge this evidence has not been published.

The most recent discussion of the age of these rocks is provided by Cookson and Eisenack (1961). In a study of microplankton and pollen from the Rottnest Island bore to the west of Perth, they state (p. 47): "Although the evidence . . . is inconclusive, it shows that the Rottnest deposits are Eocene and clearly younger than the Paleocene to Lower Eocene Pebble Point Formation of Victoria . . . The Upper Eocene age suggested by Belford for the Rottnest Bore deposits on the basis of foraminifera is not incompatible with their pollen and microplankton content, but it is equally possible that they may have been older than this". The material studied by Cookson and Eisenack came from between 1480 and 1595 feet; there is no reason to doubt the continuity of this deposit with the King's Park Shale on the nearby mainland.

It is clear that several workers regard Parr's original age determination as being too young. Mr. B. E. Balme (Dept. Geol., Univ. W. Aust.) has kindly informed the writer (pers. comm.) that a Paleocene age makes interpretation of the palynological evidence very much easier.

## Correlation and Age of the King's Park Shale

*Note on comparison with Upper Eocene faunas.*—Several species occurring in the fauna are found also in various firmly dated Upper Eocene sediments. However, an inspection of several Upper Eocene faunas, particularly those from the Brown's Creek Clays in western Victoria, has shown that the resemblances are less striking than Crespin and others have implied. In the absence of monographic studies, the true faunal relationships cannot be fully demonstrated. But we may note a few examples of alleged occurrences of King's Park species in the Upper Eocene (e.g. Carter 1958) which are based on misidentification (the Eocene species will be discussed elsewhere):

*Bolivinopsis crespinae* Parr.
*Alabamina westraliensis* (Parr).
*Chiloguembelina rugosa* (Parr).

More significantly, several important Upper Eocene species (see Parr 1947, Carter 1958, Glaessner and Wade 1959, Ludbrook 1963) are not found in the King's Park Shale. Among others in this category, there are:

*Globigerapsis index* (Finlay).
*Pseudohastigerina micra* (Cole).
*Hantkenina alabamensis compressa* Parr.
*Asterigerina adelaidensis* (Howchin).
*Carpentaria hamiltonensis* Glaessner & Wade.
*Maslinella chapmani* Glaessner & Wade.
*Lamarckina airensis* Carter.

*Comparison of King's Park Shale with Australian Paleocene faunas.*—The King's Park Shale shows considerable overall faunal resemblance to the Carnarvon Basin Paleocene. Parr (1938) identified nearly 70 species in the King's Park Shale; Coleman (1952) has found more than 90. Of about 100 species found so far by the writer (unpubl. thesis) in the Boongerooda Greensand (McWhae *et al.* 1958, and refs.), more than 50 have been identified in the King's Park Shale material at hand.

About 100 species have been identified also in two Paleocene faunas from the Wangerrip Group, Otway Basin, western Victoria (Baker 1953, and refs.). Again, more than 50 occur also in the King's Park Shale. This similarity is greater than with the Boongerooda Greensand because the two Victorian faunas, from the Pebble Point Formation and the Rivernook Member of the Dilwyn Clay respectively (Baker, 1953), are mutually quite distinct.

Correlation of the King's Park Shale with the sequence in western Victoria is based largely on the mutual occurrence of the following benthonic species. That some of them are very rare is of little importance; it is their presence that matters, because not one is known authentically from the Australian Upper Eocene.

*Vaginulina longiforma* (Plummer).
*Citharina subplumoides* (Parr).
*Angulogerina* sp.
"*Bolivinopsis crespinae* Parr" (believed to be *Spirobolivina emmendorferi* (Jennings)).
*Alabamina westraliensis* (Parr) (*A. wilcoxensis* Toulmin is considered a junior synonym).
*Ceratobulimina westraliensis* Parr.
*Lamarckina rugulosa* Plummer.
*Lamarckina* aff. *L. naheolensis* Cushman & Todd
*Epistominoides* aff. *E. midwayensis* Plummer.
*Anomalinoides westraliensis* (Parr) (*Cibicides danica* Brotzen is considered a junior synonym).

As well as providing a firm basis for correlation within the Australian region, this list of species suggests most strongly that the King's Park Shale is Paleocene in age. With the exception of *Angulogerina* sp., all these species or closely related forms are found in the Paleocene of the North American Gulf Coast (Olsson 1960, Cushman 1951 and refs.). Similarly, several occur in the Paleocene of Scandinavia (Brotzen 1948) and Poland (Brotzen and Pozaryska 1957, 1961). *Lamarckina rugulosa* perhaps is the most significant Paleocene index fossil in the above list (see also Pozaryski and Pozaryska 1960). Only a few specimens have been found in the King's Park Shale, but *L. rugulosa* is common in the Rivernook Member of the Dilwyn Clay.

*Planktonic species and their significance.*— The King's Park Shale is less rich in plankonics than the Boongerooda Greensand, which is "Tethyan" in its species diversity and large numbers of specimens. Nevertheless the planktonics are the most conclusive evidence for dating the formation. The following elements have been identified:

- *Globorotalia chapmani* Parr (60 specimens).
- *Globorotalia pseudomenardii* Bolli (2 specimens).
- *Acarinina mckannai* (White) and related forms (relatively common).
- *Globigerina linaperta* Finlay species group.
- *Chiloguembelina crinita* (Glaessner) (20 specimens).
- *Chiloguembelina trinitatensis* (Cushman & Renz) (2 specimens).
- *Zeauvigerina aegyptiaca* Said & Kenawy (3 specimens).

In 1957 Bolli published a detailed zonation of the Lower Tertiary Lizard Springs Formation of Trinidad, with five zones spanning the Dano-Paleocene interval. This zone sequence has been extended to other sections in Europe and the Americas, unaltered or in somewhat modified form, and the writer has used it in the Carnarvon Basin Paleocene. The zone sequence for the Dano-Paleocene, as modified by Berggren (1964), is as follows:

- *Globorotalia velascoensis* Zone
  - *Globorotalia velascoensis* subzone.
  - *Globorotalia pseudomenardii* subzone.
- *Globorotalia pusilla pusilla—Globorotalia angulata* Zone.
- *Globorotalia uncinata Zone.*
- *Globigerina daubjergensis—Globorotalia trinidadensis* Zone.

For the purpose of this discussion, the *G. velascoensis* Zone is equated with Upper Paleocene.

It has become clear over the past few years that *Globorotalia chapmani,* masquerading as "*Globorotalia elongata* Glaessner", etc. (see p. 85), is restricted in its total range to the upper part of the Paleocene. The only significant occurrence of *G. chapmani* in apparently younger sediments was in the Nanafalia Formation at the base of the Wilcox in Alabama, dated as basal Eocene by Loeblich and Tappan (1957). The Nanafalia, however, is Paleocene, in the *G. Pseudomenardii* subzone (Bramlette and Sullivan 1961, Gartner and Hay 1962, Berggren 1964). *Globorotalia chapmani* first appears in the *G. pusilla pusilla-G. angulata* Zone, and occurs most commonly in association with *G. pseudomenardii,* as in the Boongerooda Greensand. There are records from the *G. velascoensis* subzone (e.g. Hay 1960) though the species is not found in the highest known Paleocene in the Carnarvon Basin. Thus its appearance at depth in the King's Park Shale (South Perth 1505 ft., Langley Park 951 ft.) and its range up to and including the highest samples available (King's Park 120 ft., King's Park No. 2 150 ft., Langley Park 208-224 ft.) is decisive for age and correlation.

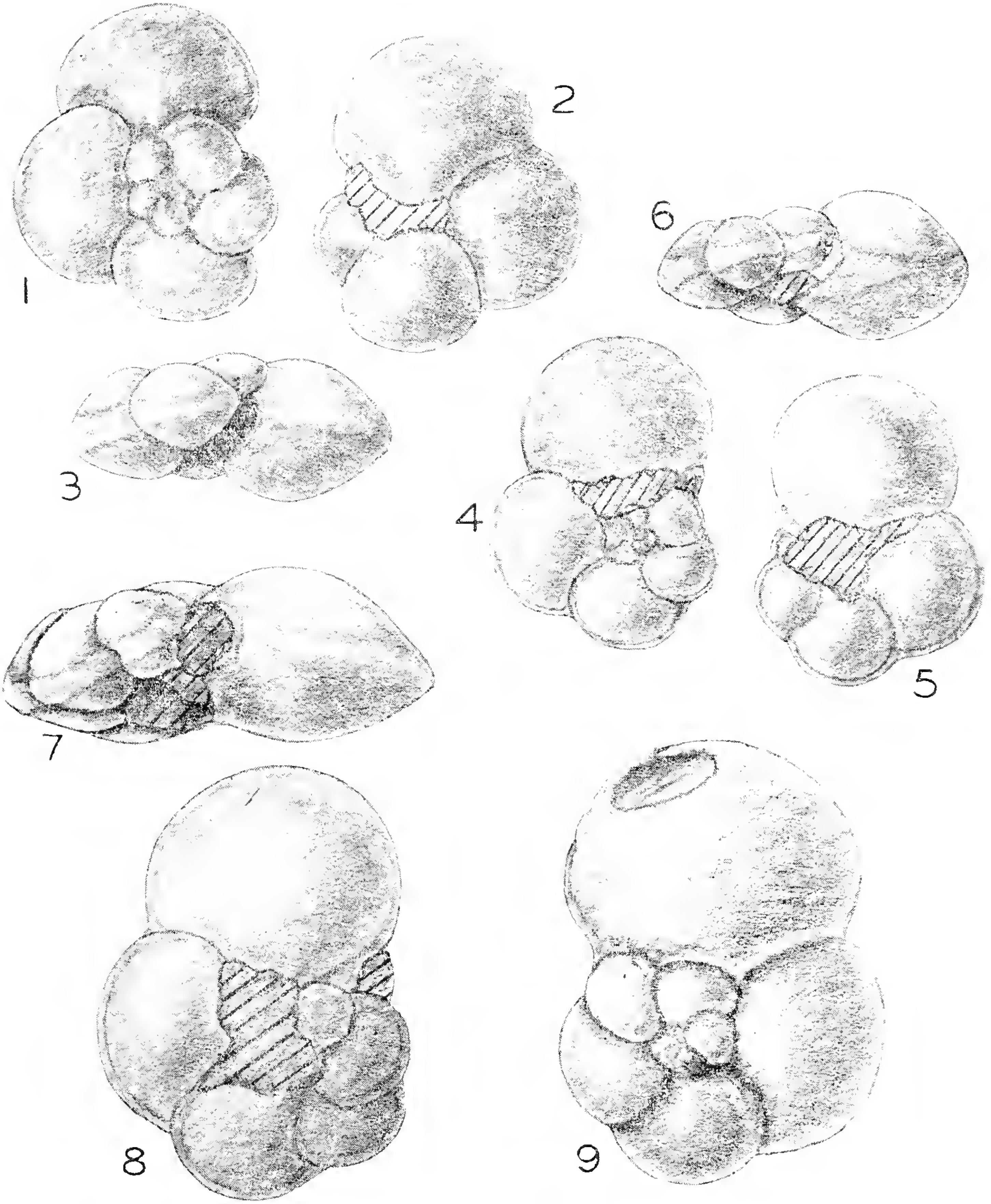
The occurrence even of two specimens of *Globorotalia pseudomenardii* (Langley Park 400 ft., 208-224 ft.) also is significant. Gartner and Hay (1962) have emphasized the wide distribution and restricted range of *G. pseudomendardii.* Whether the species always is restricted to the *G. pseudomenardii* zone as defined by Bolli (1957, see also Bolli and Cita 1960, Hay 1960) is not quite clear. It seems probable that like *G. chapmani,* it persisted with restricted numbers and distribution into the *G. velascoensis* subzone. While common in the Boongerooda Greensand and its deeper water equivalents in the Carnarvon Basin, *G. pseudomenardii* is represented in the highest Paleocene only by a few small specimens.

A Paleocene age is supported by the remaining planktonic elements of the King's Park Shale fauna. These species occur in the Boongerooda Greensand together with additional species not found in the King's Park Shale. The variable species group referred tentatively to *Acarinina mckannai* (White) (see von Hillebrandt, 1962, Gohrbrandt, 1963, and references therein) includes also morphotypes which have been identified by some workers under other names; but all are characterized by reniform chambers in a low to (particularly) high spired arrangement. Large samples of well preserved material are needed to study this variation adequately. The presence of this group suggests the *G. velascoensis* Zone (*s. l.*) equivalents without definitely excluding Lower Eocene. More locally, however, the group is restricted in the Carnarvon Basin like *G. chapmani,* being abundant in the *G. pseudomenardii* subzone but not occurring higher. The Middle Eocene index species *Globigerina orbiformis* Cole ( *Porticulosphaera mexicana* (Cushman)), as identified and figured by Parr (1938), belongs to *A. mckannai.*

*Gümbelina venezuelana* Nuttall var. *rugosa* Parr 1938 is a junior synonym of *Gümbelina crinita* Glaessner 1937. The occurrence of *Chiloguembelina crinita, Ch. trinitatensis* Cushman & Renz and *Zeauvigerina aegyptiaca* Said & Kenawy support the evidence cited above still further. Beckman (1957) has studied the distribution of *Chiloguembelina* etc. in the Trinidad Lower Tertiary, with reference to Bolli's zone sequence. He has found that the three species listed are restricted to the Upper Paleocene. Other records (Loeblich and Tappan 1957, Said and Kerdany 1961) support this.

### General Discussion and Conclusions

An analysis of the planktonic foraminiferal fauna, particularly the occurrence throughout of *Globorotalia chapmani,* has shown that the King's Park Shale is Paleocene in age. The same evidence, however, is not good enough to indicate positively the interval spanned in terms of the biostratigraphic sequence currently used. But it is likely that most of the formation was restricted in time of deposition to the *Globorotalia pseudomenardii* subzone. The fauna, particularly the presence of the *Acarinina mckannai* species group throughout, suggests the absence of the *G. pusilla pusilla-G. angulata* Zone. And apart from the long-ranging *Globigerina linaperta* species group, the King's



*Globorotalia chapmani* Parr. 1, 4, 8, 9: spiral views; 3, 6, 7: edge views; 2, 5: umbilical view. Adherent matrix indicated by diagonal ruling. 1-3.—(52643) Claremont Bore, 300-350 ft. 4-6.—(52644) Langley Park Bore, 400 ft. 7-8.—(52645) Langley Park Bore, 951 ft. 9.—(18897) King's Park Bore No. 1, 755 ft. (Subsidiary specimen figured by Parr, 1938, pl. 3, fig. 8; here refigured). Registered numbers: Geology Department, University of Western Australia. All specimens from Parr Collection therein. All figs. X132.

Park species are not found in *G. velascoensis* subzone equivalents in the Carnarvon Basin, but they are all present (except perhaps *Ch. trinitatensis*) in the Boongerooda Greensand and other *G. pseudomenardii* subzone equivalents.

The King's Park Shale can be correlated with the Otway Basin Paleocene in Victoria on the basis of several mutually occurring benthonic species which have been found also in the Paleocene of Europe and North America. These species do not have the biostratigraphic precision of the planktonics at present, but the fauna as a whole decidedly is Paleocene in general aspect. Of course, some species extend into the Eocene. The only definite Lower Eocene foraminiferal faunas known at present in Australia occur in the Carnarvon Basin, where planktonic index species have been found by Glaessner (McWhae *et al.* 1958) and the writer. The King's Park Shale contains no species which could suggest a definite correlation with these faunas or with the more widespread and sometimes rich Middle to Upper Eocene faunas. All the species in common have unknown but long stratigraphic ranges. Hence all the negative evidence available, that is, the absence of Eocene planktonic and significant benthonic species, supports the positive evidence embodied in the presence of Paleocene planktonic and benthonic species in the King's Park Shale.

We have discussed the Paleocene only with reference to its zonal subdivision. The use of stage names has been avoided; this subject is in a state of flux and is outside the scope of the present paper. It is sufficient to date the King's Park Shale as Upper Paleocene, definitely younger than Danian and Lower Paleocene.

These conclusions are more definite than those reached by Cookson and Eisenack (1961). Cookson and Eisenack compared the Rottnest bore microplankton and microflora with Cookson's "Microflora C" of the Victorian Lower Tertiary (Cookson 1954), particularly by the presence of the pollen species *Proteacidites pachypolus* Cookson and Pike. "Microflora C" is of indefinite Lower Tertiary age, though definitely younger than the Pebble Point Formation in Victoria. The Pebble Point Formation has been regarded as Lower Eocene with Paleocene affinities by Baker (1953 and refs.) who relied on somewhat inconclusive studies of its molluscan and foraminiferal content by Teichert, Singleton, Glaessner and Parr; and Cookson and Eisenack have assumed a Paleocene to Lower Eocene age on this basis, not on the basis of its microflora or microplankton content. A study of the Pebble Point foraminifera by the present writer has suggested a correlation with the *Globorotalia pusilla pusilla-G. angulata* Zone, slightly older than the *Globorotalia pseudomenardii* subzone. A Middle Paleocene age is supported also by the correlating of the Rivernook Member of the overlying Dilwyn Clay with the *Globorotalia velascoensis* subzone or uppermost *G. pseudomenardii* subzone, that is, Upper Paleocene. Thus, it appears on biostratigraphic evidence that "Microflora C" in part is of Upper Paleocene age. On the other hand, the interval under consideration in the Rottnest Is. bore (1480 to 1595 feet) may be younger than the King's Park Shale as developed beneath Perth, but this is most unlikely unless the beds dip steeply to the west (indeed, Coleman (1952) states that an easterly dip is possible) or are faulted.

## Notes on Species

### *Globorotalia chapmani* Parr

Pl. 1, figs. 1-9.

*Globorotalia chapmani* Parr, 1938, p. 87, pl. 3, fig. 8, 9.

*Globorotalia membranacea* (Ehrenberg); Glaessner, 1937b, p. 385, pl. 4, fig. 38; Subbotina, 1953, p. 205, pl. 16, fig. 7-10.

*Globorotalia elongata* Glaessner; Bolli, 1957, p. 77, pl. 20, fig. 11-13; Loeblich and Tappan, 1957, p. 189, many figs.

*Globorotalia pseudomenardii* Bolli; Nakkady, 1959, p. 462; pl. 4, fig. 3.

*Globorotalia troelseni* Loeblich & Tappan; Gohrbandt, 1963, p. 51, pl. 6, fig. 13-15 (synonymy).

Parr's species has been overlooked consistently by recent students of Lower Tertiary faunas, presumably because of the misleading title of his paper. Parr's description of *Globorotalia chapmani* is given in full:

"Test biconvex, oval, the dorsal surface more convex than the ventral, which is umbilicate; periphery lobulated, peripheral margin rounded; chambers comparatively few, not more than five in the last-formed whorl, each much larger than its predecessor; sutures depressed, not limbate, gently recurved on both sides of the test; wall smooth and punctate, with a silvery lustre; aperture an elongate slit with a slight lip, opening at the base of the last-formed chamber into the umbilical depression. Length up to 0.65 mm".

Notes on Morphology.—*Globorotalia chapmani* is characterized by an imperforate marginal band which gives the impression of being a keel, but oriented thin sections show that the wall is not thickened in any way in this region.

The test varies somewhat in plan, from almost equilateral to strongly elongate due to variable increase in chamber size. The chambers of *G. chapmani* vary in inflation and the sharpness of the periphery, but typically they have an equally biconvex arrowhead shape in profile, and the early chambers usually are depressed below the outer whorl. In some individuals this is not so: the inner whorls are raised giving a broadly convex spiral surface. On both sides the sutures are distinctly depressed.

Remarks.—A metatype of *Globorotalia pseudoscitula elongata* Glaessner (collection of M. F. Glaessner) is very similar to juveniles of *Globorotalia pseudomenardii* Bolli. Russian workers (e.g. Shutskaya 1956) no longer distinguish the variety *elongata* formally from *pseudoscitula*. This species is quite distinct from "*Globorotalia elongata*" of recent workers (see also Gohrbandt, *l. c.*).

"*Globorotalia elongata*", as figured by Loeblich and Tappan, Bolli, and others, is quite variable in profile due to variation in compression of chambers and angularity of margin. Specimens from the Salt Mountain Limestone, Alabama, examined through the kindness of Prof. L. D. Toulmin (Tallahassee, Florida) show clearly that this form is *G. chapmani*.

Specimens of *Globigerina compressa* Plummer (Upper Midway, Lockhart, Texas, coll. H. J. Plummer, in collection of M. F. Glaessner) have been examined. They are smaller than *Globorotalia chapmani*. The chambers become distinctly compressed in the adult stage but they are more rounded in profile than in *chapmani*, and the margin lacks the imperforate zone (see also Hofker, Nat. Maandblad, 47:3-4, 1958).

Crespin (1954; Raggatt and Crespin 1955) has recorded *Globorotalia chapmani* from the Upper Eocene of Southern Australia. In the absence of description or figures, it is not known to which species she was referring. *G. chapmani* has not been seen in any of the material at hand from the same formations, and Carter (1958) did not mention its presence in Victoria. Possibly Crespin was referring to *Pseudohastigerina*.

Occurrence.—In several samples; 60 specimens examined.

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# 14.—Projasus—a New Generic Name for Parker's Crayfish, Jasus parkeri Stebbing (Palinuridae : "Silentes")

By R. W. George* and J. R. Grindley†

*Manuscript received—19th May, 1964*

The family Palinuridae is divisible into the Stridentes (producing sound by antennal movement) and the Silentes.

*Jasus parkeri* Stebbing, belongs to the Silentes and because of its uniqueness warrants the erection of a new genus. *Projasus* gen. nov. is intermediate between the other two genera of Silentes, *Jasus* and *Palinurellus*.

A key to the genera of Silentes is included.

## Introduction

Stebbing (1902) originally placed his new South African species, *parkeri*, in the genus *Jasus* but commented "there is no resemblance so far as I know to any other living Palinurid hitherto described". On the basis of Stebbing's description and figure alone. Holthuis (1946 : 148) considered the species "no *Jasus* at all" and allocated it to the genus *Puerulus* commenting ". . . it has for instance, a distinct stridulating organ, which is entirely absent in the genus *Jasus*". Barnard 1950 : 541) replaced *parkeri* in the genus *Jasus* stating that the stridulating organ is not present, but also recognised that ". . . there is a close resemblance to *Panulirus* [= *Puerulus*] *angulatus* Bate . . .".

Parker, in his excellent papers (1883 and 1884) on the classification of palinurids, divided them into two categories the "Silentes" and the "Stridentes". The ability to produce sound by rubbing a process of the antenna over a raised ridge on the antennular plate has been used extensively in keys and descriptions, yet few workers have adopted Parker's terminology for the two distinct groups. These terms, "Silentes" for the non-stridulating, and "Stridentes" for the stridulating group are very apt and their use is to be encouraged.

This paper presents the results of re-examination of Stebbing's and other specimens of *parkeri* from the South African Museum and concludes that the species *parkeri* does not belong to either *Jasus* or *Puerulus* but to a new genus of the Silentes, *Projasus* gen. nov.

We are very appreciative of Dr. Holthuis' assistance and comments in the final stages of preparation of the paper.

## Projasus gen. nov.

Type. *Jasus parkeri* Stebbing, 1902.

*Diagnosis.*—This genus consists of one species *parkeri* and it differs from all other Palinuridae in possessing four longitudinal rows of spines, separated by smooth regions on the carapace. It differs from the other genera of Silentes in combinations of characters as discussed below.

*Description.*—

i Antenna articulated simply; stridulating organ absent.
ii Carapace with angular sides and with longitudinal spiny ridges, otherwise smooth.
iii Abdomen smooth, first five segments with median carina.
iv Supraorbital processes pointed, unarmed and obliquely erect.
v Eyes produced laterally on eyestalks, not recessed.
vi Median rostrum and clasping processes very small.
vii First abdominal segment of female without pleopod.

*Remarks.*—Parker (1883 and 1884) recognised only one species group in the Silentes and for this group he proposed the sub-genus *Jasus*. Although he did not tabulate *Palinurellus* Von Martens 1878 in his Silentes group (1884, p. 304), he clearly recognised its lack of a stridulating organ and suggested that it was close to the "parent species" of the family Palinuridae (1884, p. 303). *Palinurellus* is now recognised (see Holthuis 1946) as an actual member of the Palinuridæ.

Parker's original concept of *Jasus* was based on the species *lalandii* H. Milne Edwards, 1837; *edwardsii* Hutton, 1875 and *hugelii* Heller, 1862 (this species is now regarded as a synonym of *verreauxii* H. Milne Edwards, 1851; see Holthuis 1946). These non-stridulating species form a natural group having in common a cylindrical, uniformly spiny carapace and abdominal terga without median carina, either smooth (*verreauxii*) or with squamiform sculpture (*lalandii* group). *Projasus* gen. nov. is therefore clearly outside the boundaries of the *Jasus* species group as envisaged by Parker (cf. ii, iii. above).

*Palinurellus* bears a general resemblance to *Projasus* in the possession of median, but less pronounced, carinæ on the abdominal terga. However, *Palinurellus* has no spines on the carapace, and no supraorbital processes, the eyes are simply recessed at the sides of a large rostrum which lacks clasping processes; the first abdominal segment of the female possesses a pleopod (Holthuis pers. comm., 1964) (cf, iv, v, vi, vii above).

Both Holthuis (1946) and Barnard (1950) noted the close general resemblance of *parkeri* to *Puerulus* (one of the Stridentes), presumably based on the angular shape of the carapace. The absence of a stridulating organ however easily separates *Projasus parkeri* from all Stridentes and places it in the Silentes group.

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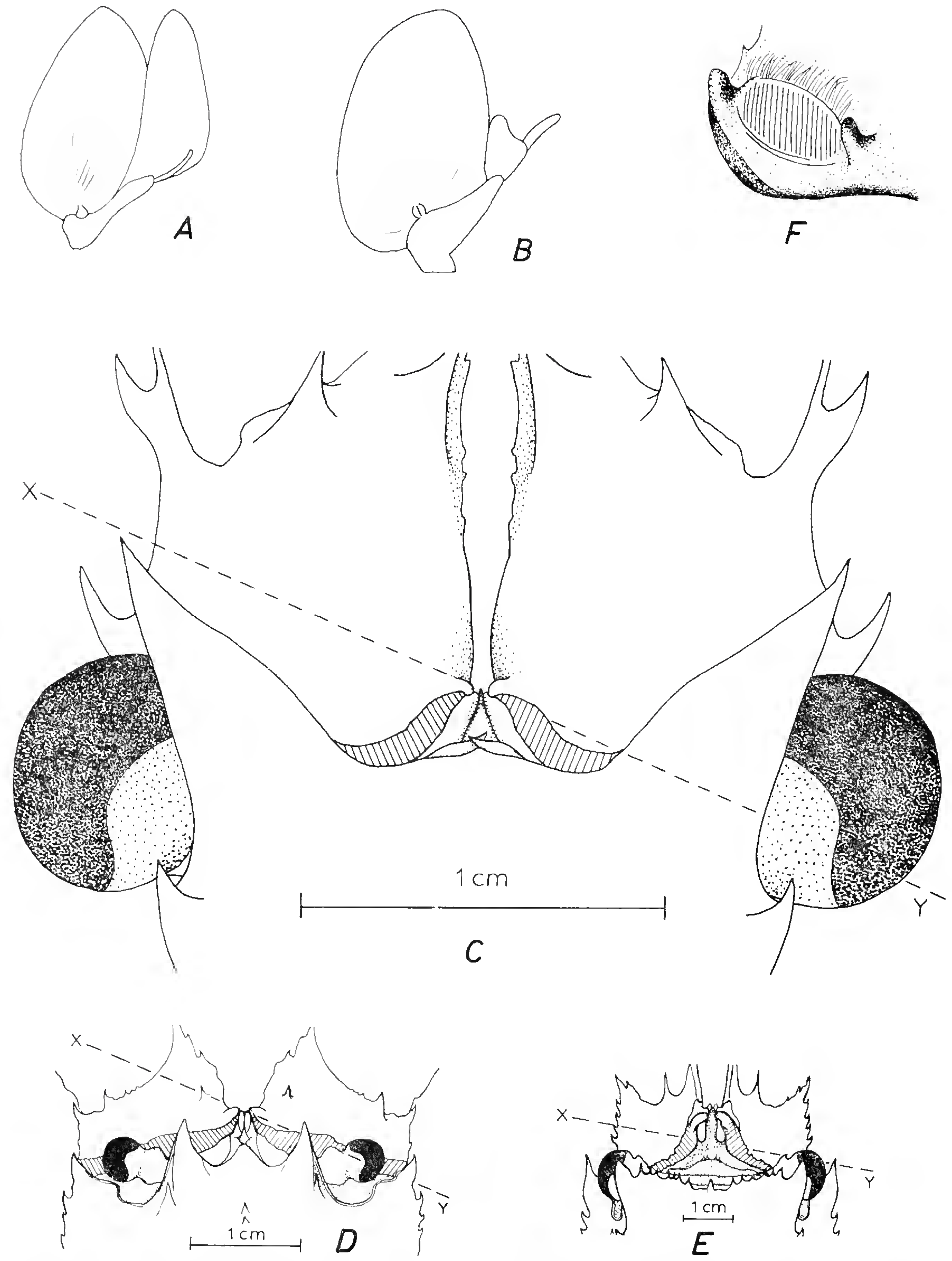

Fig. 1.—A, B, C, *Projasus parkeri;* A, female pleopod of second abdominal segment B, female pleopod of third abdominal segment C, anterior region of carapace. D, *Jasus lalandii* anterior region of carapace. E, F, *Palinurus gilchristi;* E, anterior region of carapace F, underside of stridulating pad. X-Y indicates axis of antennal articulation.

We regard *Projasus* as a genus of Silentes intermediate between *Palinurellus* and *Jasus*. It differs as much from the other genera of Silentes, as *Puerulus* does from the other genera of Stridentes.

### Key to the Genera of Silentes Palinurids

| | | |
|---|---|---|
| (1) | Supraorbital processes present; median rostrum and clasping processes small; carapace with spines | 2 |
| | Supraorbital processes absent; median rostrum large; clasping processes absent; carapace with low tubercles | *Palinurellus* |
| (2) | Carapace with rounded sides and covered with many subequal spines; abdomen smooth or squamiform | *Jasus* |
| | Carapace with angular sides and with longitudinal spiny ridges; abdomen with median carina | *Projasus* |

This key is based on our examination of all taxa of Silentes recognised by Holthuis (1946 and 1963) except *Palinurellus gundlachi* and *Palinurellus gundlachi* var *wienecki*.

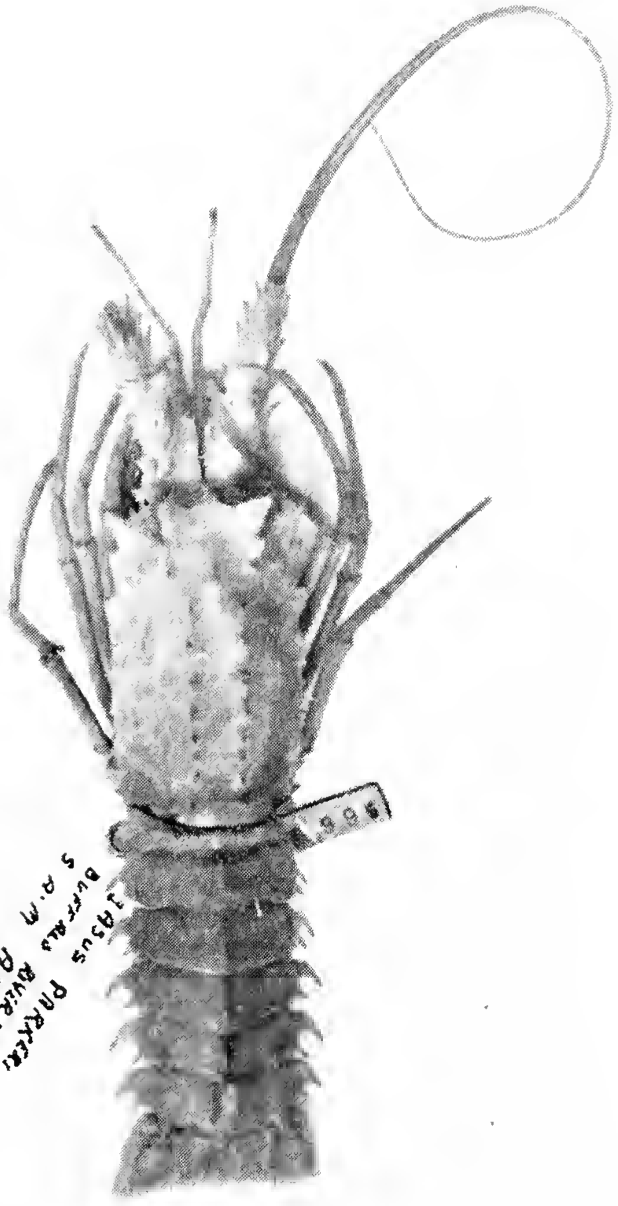

Fig. 2.—*Projasus parkeri* female, carapace length 58 mm, off Buffalo River, South African Museum No. A995, now housed in Western Australian Museum.

### Projasus parkeri (Stebbing)

(Figs. 1 A, B, C, and 2.)

*Jasus parkeri* Stebbing 1902 p. 39, pl. 7 and 1910 p. 375; Barnard 1950 p. 540.

*Puerulus parkeri;* Holthuis 1946 pp. 110 and 148.

*Type Locality.*—". . . shrimp trawl, Buffalo River north 15 miles. Depth, 310 fathoms. Bottom, coral and mud". [lat. 33°S. long. 28°E.]

*Description.*—The original description and figure given by Stebbing (1902) require little amplification. Only two features are redescribed here—the female pleopods and various structures in the anterior region of the carapace.

In his key to the genera of Palinuridae, Holthuis (1946 p. 113) indicated the value of the shape of the various female pleopods as taxonomic characters and illustrated fifteen pleopods of several species but *parkeri* was not among these. Stebbing (1902) and Barnard (1950) gave only brief descriptions of the female pleopods but did not illustrate them.

Because of the lack of detail in the anterior region of the carapace in Stebbing's (1902) original illustration of *parkeri*, Holthuis (1946) interpreted the exaggerated ridges of the antennular plate as part of a stridulating mechanism. As a result he incorrectly allocated it to the genus *Puerulus*.

*Female pleopods* (fig. 1A and B).—There are no appendages on the first abdominal segment. The endopod of the pleopod of the second segment is almost as large as the exopod and bears a reduced stylamblys (fig. 1A). On the third, as on the fourth and fifth abdominal segments, the endopod of the pleopod is not foliate and the stylamblys is present (fig. 1B).

*Anterior region of carapace, fig. 1C.*—The rostrum is small, acute, upturned and embraced by two small, pointed clasping processes. The narrow antennular plate runs forward and downward and its exposed sides are longitudinally convex. The articulating process of each antenna abutts the latero-distal region of the antennular plate and merely pivots on it when the antenna is raised.

#### Comparison of Silentes and Stridentes

In the Silentes, the sides of the antennular plate are not well developed or polished and the axis of articulation of the antenna passes through the point of articulation of the antennal process with the antennular plate. Due to the simple rotation of the antennal process, no sound is produced when the antenna is raised. The axis of articulation of the antenna is indicated by the oblique broken lines X-Y for *P. parkeri* in fig. 1C and for *Jasus lalandii* in fig. 1D.

On the other hand, the Stridentes have highly polished areas on the sides of the antennular plate and well developed lateral processes on the antennae. These processes have a ribbed pad on their under surface and the axis of articulation is nearly transverse. When the antenna is raised, the ribbed stridulating pad moves over the polished area on the side of the antennular plate producing the characteristic stridulation of the Stridentes group. In figs. 1E and F. the anterior region and the underside of the stridulating pad of *Palinurus gilchristi* is illustrated. The genus *Panulirus* with its very broad antennular plate probably represents the greatest development of the stridulating apparatus.

The Silentes however, are not without means of sound production. A. Heydorn of the Division of Sea Fisheries, South Africa, reports that *Jasus lalandii* makes loud "clicking" noises under water without movement of the antennae and believes that the sound is probably produced by the mandibles.

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# Memorial

## Douglas Elwood White

Douglas Elwood White — M.Sc., Ph.D., F.R.A.C.I,. died as the result of a car accident on the evening of 4th April, 1964, at the early age of 53 years.

His long association with the University of Western Australia where he was Professor of Organic Chemistry at the time of his death, was largely responsible for the expansion of organic chemistry in this State during the post-war years.

He graduated from the University of Sydney with first class honours in 1930 and completed his M.Sc. in 1932. He later went on to Oxford where he worked in the Dyson Perrins Laboratories and was awarded the degree of Doctor of Philosophy in 1937.

White first lectured in Organic Chemistry at the University of Sydney and was then appointed biochemist to its School of Public Health and Tropical Medicine. In 1941 he became lecturer in Organic Chemistry at Melbourne University and in 1943 joined the University of Western Australia as Lecturer in Charge of the same discipline. He was appointed Reader and Head of this Department in 1945 and in 1958 became the University's first Professor of Organic Chemistry.

His early research on essential oils developed into the broader field of plant chemistry particularly in relation to the flora of this State. His varied contributions to science covered work on tannins, coumarins, alkaloids, terpenoids and the oestrogenic isoflavones of sub-terranean clover.

A period of study leave in 1950-51 was spent at the Technical High School, Zurich, where White developed a specialised interest in polyterpenes on which he later became an authority.

Despite his great interest in research, he was an able administrator and served as the Dean of the Faculty of Science from 1957 to 1959. He gave freely of his time to a number of scientific societies and was chairman of the organising committee of ANZAAS for the Perth Congress in 1959. In his long association with the Royal Society of Western Australia he acted on the Editorial Committee from 1954 to 1957, was a Council member in 1953-54, Vice President in 1954-55 and President in 1955-56.

# 15.—Geographical Variation and Distribution of some Birds from Western Australia

By G. F. Mees*

*Manuscript received—17th March, 1964*

Revisional and distributional data are given on ten species of passerine birds from Western Australia.

### Introduction

Over the past few years I have collected evidence on the validity of certain subspecies of birds described from Western Australia, together with other information. Some of these findings alter or are complementary to recent revisions (Mayr 1948, 1954, Mees 1961), and therefore warrant publication. All material discussed is in the collection of the Western Australian Museum.

### **Coracina novaehollandiae** (Gmelin)

Earlier I stated that no evidence of migratory movements in Western Australia existed (Mees 1961, p. 111), and that no individuals of *C.n. melanops* were known from within the range of *C.n. subpallida*.

However, in July 1959 I was surprised to find flocks comprising dozens of birds in the scrub-country south of Carnarvon; there were individuals with dark and with pale mantles, clearly both *melanops* and *subpallida*. In the first fortnight of August 1959, the species was also common at North West Cape, though not in such great numbers. The concentration of hundreds of birds near Carnarvon was far above anything one would expect of a local breeding population or even of local movements, and I am convinced that true migration was involved. On 14 May, 1960 I especially noted that in the same area not a single individual was observed. In December 1962 I saw only an occasional pair of what seemed to be *subpallida*. According to Peters & Mayr (in Mayr & Greenway 1962, p. 171), *subpallida* winters in the Lesser Sunda Islands and Kei Islands. It may be that the subspecies does partially migrate to these islands, but I have not seen specimens, and the majority of individuals seems to stay in Australia.

Material collected since my previous paper was written confirms the occurrence in winter of both subspecies in the north-west of the State. I give here a full list of specimens and localities.

*C.n. subpallida.* ♀, 5-VIII-1959, Milyering Well, Yardie Creek Station, North West Cape (A 8636); ♀, 20-V-1960, Cossack (A 8526); ♂ imm., 20-V-1960, Cossack (A 8524); ♂ 20-V-1960, Cossack (A 8525); ♀ 8-IX-1959, Edmund Station, Barlee Range (A 8649).

*C.n. melanops.* ♂ imm., 5-VIII-1959, Milyering Well, Yardie Creek Station, North West Cape (A 8924); ♀ imm., 7-VIII-1959, Milyering Well, Yardie Creek Station, North West Cape (A 8925); ♀ 11-VII-1959, Murchison River Bridge, north of Geraldton (A 8953); ♂, 11-VI-1962, Legendre Island, Dampier Archipelago (A 8835); ♂ 22-I-1962, Beagle Bay Road, west Kimberley Division (A 8951); ♂ 21-VI-1960, Kalumburu, north Kimberley Division (A 8622).

Note especially the specimens of *melanops* from Yardie Creek and Legendre Island, in the range of *subpallida*. The specimen from the Murchison River is rather pale for *melanops* and may be considered somewhat intermediate: this is what one would expect from a breeding bird of that locality. Keast (1961, p. 413) refers to the form *subpallida* as an isolate, but I regard it is unlikely that it is.

Previously I noted that the testes of *C. novaehollandiae* are dark slate in colour. I have since collected *Coracina papuensis hypoleuca* in the Kimberley Division (Kalumburu and Beverley Springs) in which I found the same feature.

### **Acrocephalus stentoreus gouldi** Dubois

Mayr (1948), in his revision of the Australian reed-warbler, accepted as valid the name *carterae* Mathews, though with grave misgivings: " . . . the type of *carterae* has a relatively and actually much larger bill than *gouldi*. I would refrain from naming a new form on such slight basis and with only a single specimen available, but now that the name is in the literature, it must be recognized". A specimen collected by me near Derby on 6 June, 1960, almost topotypical of *carterae*, has a bill of average length for *gouldi*, from individuals of which race I am unable to distinguish it. Moreover, in June 1962, during a visit to the American Museum of Natural History, I compared the type of *carterae* with specimens from south-west Australia, and found a south-west bird with a bill as long as the bill of *carterae*. Therefore, *carterae* is doubtless a synonym of *gouldi*. At the time of my visit to Derby, the small pool where I collected a specimen harboured several individuals, but my friend Mr. P. Slater, at the time a resident of Derby, who accompanied me, mentioned that he had not previously observed reed-warblers in that locality. I regard it as possible that the birds observed were migrants from the south. As yet there is no proof of the existence of an indigenous breeding population in the Kimberley Division.

The validity of *gouldi* itself is in need of confirmation, as I have pointed out in a previous paper (Mees 1961, p. 113).

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**Pachycephala pectoralis** (Latham)

According to the latest published information, in south-western Australia this species extends from the mouth of the Murchison River to the Esperance area, and inland to Bunketch (observed once), Kellerberrin (rare), Lake Grace and Mt. Ridley (Reid 1951, Ford & Stone 1957, Serventy & Whittell 1962).

In the first half of 1963 I found it in several localities well inland from the range indicated, and it appears that the species is much more widely distributed than was hitherto known. The observations are as follows (Fig. 1): Mt. Hampton, 10 March, one singing male; Mt. Holland, 15 April, two singing males; Parker Range, 15 April, fairly common; Moorine Rock, 16 April, several individuals of both sexes; Carrabin, 16 April, a pair; Great Eastern Highway near the 301 mile post (47 miles west of Coolgardie), 12 June, at least two singing males; Mordetta, 10 July, several individuals; eleven miles north of Pingaring, 10 July, one singing male; Jitarning, 21 and 22 July, several individuals.

While none of these observations were made in the breeding season, nothing is known of migration, and I regard it as likely that the species is a resident in the localities listed. It is surprising that this common and familiar species has been overlooked in such an extensive part of its range.

**Pachycephala lanioides** Gould

In his review of the Australian members of the genus *Pachycephala*, Mayr (1954) recognized four subspecies of *P. lanioides*: *bulleri*, *carnarvoni* (consistently misspelt *carnavoni* by Mayr), *lanioides* and *fretorum*.

Mayr did not have much material at his disposal; he was also much impressed by the patchy occurrence of mangroves along the Australian coast. Earlier Mack (1933) had been even more handicapped by lack of material. Over the past few years many additional specimens have been collected by myself and other staff members of the Western Australian Museum.

Before discussing the variation of the species, I will say something about mangrove birds in general. It is true, as Mayr states, that the occurrence of mangroves is patchy. But does this necessarily mean that Mayr (p. 10) is also right in calling the populations inhabiting such mangrove patches "true isolates"? In my opinion the problem of the mangrove birds, and of other birds inhabiting a specialised habitat which is patchy in occurrence, is to find and colonize all the available habitat, because perhaps no single patch is large enough to ensure the continued existence of a population for any great length of time. In other words, birds of this group, to be successful, must have fairly good dispersal faculties. This is in conflict with a natural tendency to become sedentary in any good patch of habitat. Probably both these opposite selective factors are at work, resulting in a species with moderate mobility. On the basis of this the geographical variation of *P. lanioides* can be explained satisfactorily. On

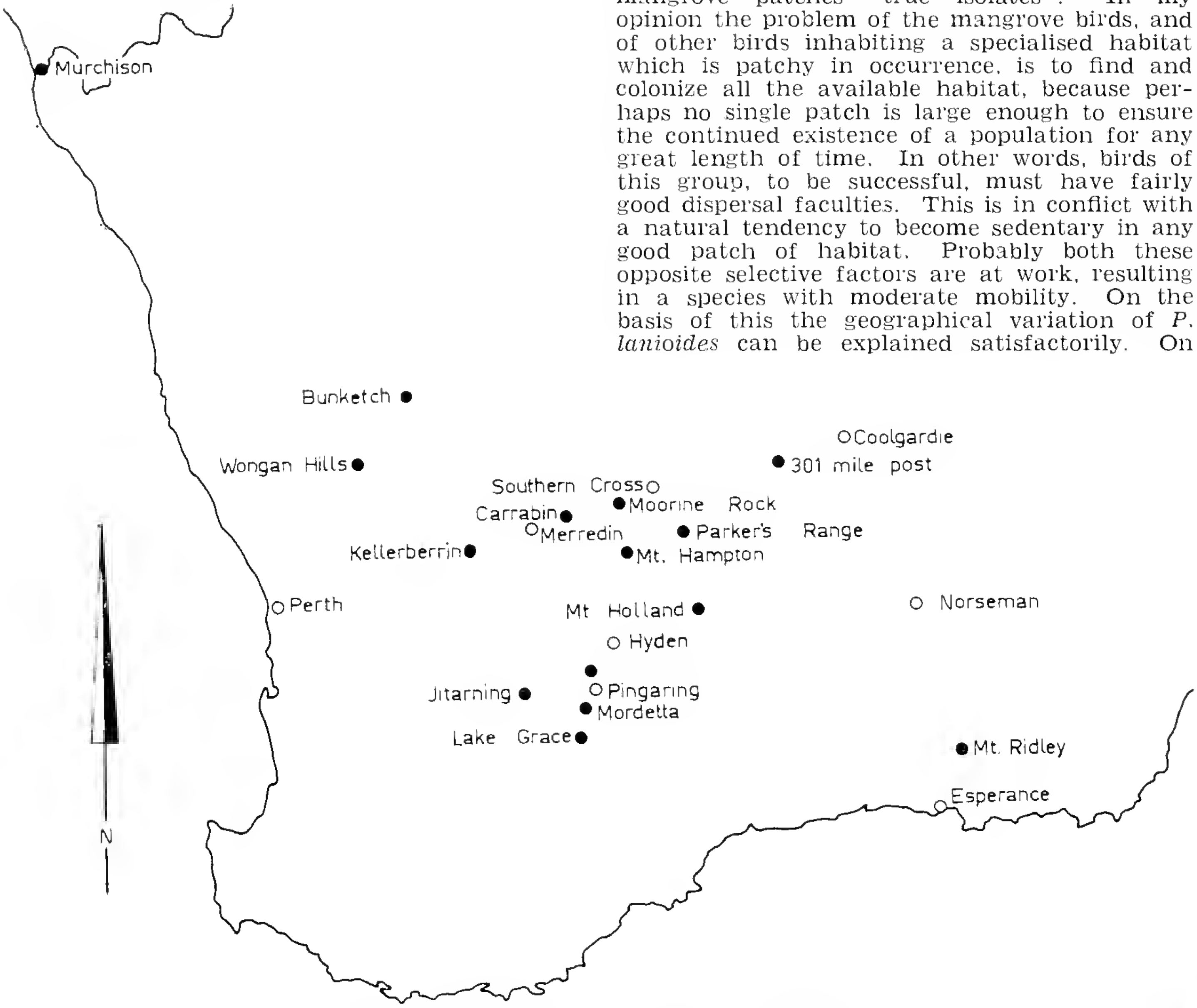

Fig. 1.—The inland distribution of *Pachycephala pectoralis* (dots) in Western Australia. Towns indicated by open circles are put in for orientation.

Fig. 2.—The distribution of *Pachycephala lanioides* (dots). The arrows with the figures 1 and 2 indicate position and extent of the two major gaps in the mangrove belt in Western Australia.

the map (Fig. 2) I have indicated the distribution of *P. lanioides* as ascertained from material examined and from Mayr's records, and also the two major gaps in the mangrove, as ascertained during visits to the north and north-west of the state in 1959, 1960 and 1962: a gap of about 220 miles between Carnarvon and Tantabiddy (North West Cape), and one of about 140 miles between Pardoo and La Grange.

The new material confirms the conclusions as regards geographic variation drawn by Mayr, except that I recognise not four, but three races, which from south-west to north-east are:

1. *Pachycephala lanioides carnarvoni* (Mathews 1913).

*Pachycephala lanioides bulleri* Mayr 1954.

Differs strikingly from the other races in that the female and the male in immature plumage are essentially brown in colour, not grey. I fail to find any differences between birds from Carnarvon, Exmouth Gulf and as far up the coast as Port Hedland (included in *bulleri* by Mayr). Most interesting is a single adult female from Pardoo, which is greyish brown in colour, almost exactly intermediate between *carnarvoni* and the nominate race. This is what one would expect from its intermediate geographical position. I have not examined topotypical material of "*bulleri*" from De Grey, but the mangroves between there and Exmouth Gulf are more or less continuous, show at least no major gaps, and in Mayr's description there is nothing inconsistent with the view that this population differs from *carnarvoni* only in a slight trend towards the nominate race, a trend more pronounced in the Pardoo bird. As in my opinion there is no point in subspecifically naming intermediates where smooth gradients exist, and as naming is in such cases actually misleading, *bulleri* has to be synonymized with *carnarvoni*, to which it is closest. I may add that I do not quite understand why under the subspecies *bulleri*, Mayr remarks: "This ecologically specialized bird is undoubtedly confined to isolated pockets of mangrove". The remark is very much to the point, but not especially for this race, but for the whole species.

Though, as Mayr pointed out, Mathews (1930, 1931) had synonymized his name *carnarvoni*, it should be noted that A. J. Campbell (1918), who was an infinitely better ornithologist than Mathews, had previously mentioned its diagnostic characters.

Measurements.—Males: 97, 97.5, 100, 100, 101, 101, 101, 102, 102, 103. Males in female plumage: 96, 96, 99, 100. Females: 93, 95, 96, 97, 98, 99, 101.

Distribution.—The coast of Western Australia from Carnarvon to De Grey; intermediates towards the following race at Pardoo.

2. *Pachycephala lanioides lanioides* Gould 1840. Males are similar to those of the preceding subspecies, females differ by being grey, not brown, above, and much paler with hardly any buff below.

Measurements.—Male, 102. Male in female plumage: 96. Female: 97.

Distribution.—Only known from the West Kimberley Division, from Broome to Point Torment, but almost certainly ranging farther north.

3. *Pachycephala lanioides fretorum* De Vis 1889. Similar to the nominate race but slightly smaller.

The four specimens taken by me at Wyndham confirm Mayr's conclusion as regards the applicability of the name *fretorum* to the slightly smaller eastern birds. At the same time it must be remarked that my material is in rather worn plumage and that the difference in size is slight. Specimens from Wyndham agree in wing size with material from the Roper River, the easternmost locality whence the species is certainly known. They also agree with the measurements published by De Vis (♂: 93, 96; ♀: 92).

Measurements.—Males: 95, 99. Females: 93, 94. The following measurements of material from Roper River in the H. L. White Collection were supplied by Mr. McEvey. Males: 94, 95, 97. Immature male: 96. Females: 92, 94.

Distribution.—Northern Australia from the Cambridge Gulf to the Roper River; apparently Kimberley, Gulf of Carpentaria.

Discussion.—Both Mack (1933) and Mayr (1954) have commented on the inadequacy and ambiguity of De Vis' (1889) description. I have studied it carefully, and in my opinion it makes sense only if in its first paragraph the word "not" is added, so that it comes to read: "Among the birds brought from Cambridge Gulf is a young female Pachycephala which is NOT identical with an adult of the same sex procured at Kimberley on the Gulf of Carpentaria in company with two males. These which have hitherto been supposed to be *P. lanoides*, Gld., must now be considered to constitute a distinct species. The writer proposes for it the name *P. fretorum*".

When this is done the description becomes understandable; the receipt of the specimen from Wyndham, which De Vis considered as typical *P. lanioides* (misspelt *lanoides* by him), was the first of the species from a western locality available to him, and enabled him to differentiate his three eastern birds from true *lanioides*. For this reason also, descriptions are given of the three Gulf of Carpentaria birds: adult male, immature male, adult female, but not of the juvenile female from Cambridge Gulf. Similarly, in the list of measurements these two males and one female are listed as *P. fretorum*, while for comparison measurements of one specimen of *P. lanioides* are given; the sex of this specimen has not been recorded again, as it had already been said to be a young female. The type locality, southern shores of Torres Straits, which would be more or less correct for the birds from Kimberley, Gulf of Carpentaria, but not for Cambridge Gulf, supports my views. So does the fact that Savilie-Kent (1889, p. 220) lists his specimen from Cambridge Gulf as *Pachycephala lanoides*, which name (with the incorrect spelling!) must have been given to him by De Vis.

On the other hand I must admit that in the list of birds collected at Cambridge Gulf (p. 236) De Vis lists this same individual as *Pachycephala fretorum*. This, however, can be ascribed to his well-known carelessness.

From the preceding discussion it will be clear that I do not regard the specimen from Cambridge Gulf as a cotype of *P. fretorum*. Kimberley, Gulf of Carpentaria, will have to be regarded as the type-locality, unless it is definitely proven that the species does not occur there. As mentioned by Mayr, the only specimen of the four discussed by De Vis now present in the Queensland Museum is the one from Cambridge Gulf. This was confirmed once more by Mr. Mack (in litt., 5-VI-1963): "I have checked the old bird collection here in connection with De Vis' species *Pachycephala fretorum*, and the only specimen present is what appears to be a young bird, possibly a female, with a culmen 20 mm. long. Originally, De Vis has written on the small label *Pachycephala "lanoides"*. The name *"lanoides"* has been marked out and *fretorum* put in its place. There are no other specimens of *P. lanioides* in the collections". It is unfortunate that none of the three individuals of *fretorum* described by De Vis can be traced; it should also be noted that he says nowhere that they were in the Queensland Museum, and I am inclined to believe that they were not, as it is unlikely that all three of them would have disappeared without leaving a trace.

How De Vis could find a culmen length of 17.0 to 19.0 mm in *fretorum* and of 25.0 mm in the individual from Cambridge Gulf is obscure. Possibly he measured the exposed culmen of *fretorum* and the entire culmen of *lanioides*, which would make it about right.

### **Colluricincla harmonica julietae** Mathews

Mathews (1942)* based the name *Colluricincla brunnea julietae* on a single individual from Sturt Creek, which was described as differing from *brunnea* in its smaller size. The type in the collection of the Western Australian Museum, regd. no. A 4004, has a wing length of 117 mm (Mathews gave it as 116), and though its plumage is abraded, even freshly moulted the wing would not have been more than one or two mm longer.

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* Serventy (1946) concluded that Mathews's paper with the description of this and other new forms was published in 1943, and at the time he was right. The International Commission on Zoological Nomenclature has since ruled, however, that circulation of author's copies and other preprints constitutes valid publication (Stoll & al. 1961), and certainly in a case like the present one, in which the exact date of publication is printed on the paper, there is no reason not to accept this date, 12th February, 1942. An interesting point that appears is that now *Cervinipitta kimbleyensis* was published earlier that the emendation *Cervinipitta kimberleyensis*, which appears on a slip circulated with the completed volume in 1943, but not with the original preprints.

Measurements of *brunnea* in our collection (specimens from Kalumburu, Wyndham, Nicholson Station, South Alligator River and Eureka) are: ♂, 127, 129, 132, 134, 134; ♀, 129, 130, 131, 134. It is clear from these measurements that Mathews was right and though personally I would not base a subspecies on a single worn individual and on geographical grounds strongly doubt its validity, now that it has been named, it cannot be rejected until additional material may necessitate a reconsideration of its validity. Perhaps it is significant that the male from Light House Rock Pool, Nicholson River, with a wing length of 127 mm, is slightly smaller than other specimens of *brunnea* examined. Nicholson River is about a hundred miles north-east of Sturt Creek, the type locality of *julietae*.

The northern populations of *C. h. rufiventris* are of about the same size as *julietae*, but they differ in being grey-backed rather than brown-backed, and though I have no hesitation in making both *rufiventris* and *brunnea* subspecies of *harmonica* the relationship of *julietae* is with the latter rather than with the former, as, indeed, one would expect on geographical grounds.

### **Melithreptus lunatus chloropsis** Gould

Gould (1848) described this subspecies from Swan River as having the unfeathered skin round the eye green, for which reason he named it *chloropsis*. Mathews (1909) named *Melithreptus whitlocki* from Wilson's Inlet as having the skin round the eye white all year. It may be pointed out that the names given by Mathews before his notorious contribution of January 1912, are usually valid, and the existence of two races, one with white and one with green over the eye, in the south-west of Western Australia has been accepted by several subsequent authors (Whittell & Serventy 1948, Serventy & Whittell 1951, but corrected by Serventy & Whittell 1962). I have observed and collected specimens in various parts of Western Australia, both near Perth and along the south coast, and found that in adult birds of both sexes the lunate patch over the eye is always white, while the lower eyelid is greyish blue in colour. In juvenile birds, on the contrary, which are easily distinguished by having a brownish tinge on the mantle and by the brown, not black, crown, the skin above the eye is pale blue. Gould's statement to the contrary, the skin is never green. It is clear, therefore, that Western Australia is inhabited by one race only, which retains the misnomer *chloropsis*. The nominate race differs by having the skin above the eye orange, and by its very slightly shorter bill.

### **Meliphaga virescens** (Vieillot)

The geographic variation of this species, which has a continuous range over the whole of Australia, is so gradual that it is impossible to express it satisfactorily in nomenclature. The main trend is one of larger size and darker colour towards the south and the coastal areas, and of smaller size and paler colour inland and north. In a case like this, where no sharp boundaries exist anywhere, it is wise to refrain from giving too many names. In a previous paper (Mees 1961) I commented on the large size of the type of *lewisi* from Lewis Island, Dampier Archipelago. The bird, sexed as a female, has a wing of 96 mm.

In 1962 a collecting party from the Western Australian Museum visited the Dampier Archipelago, and obtained a number of specimens of *M. virescens*, though unfortunately none on Lewis Island. Wing-lengths of this material are: Legendre Island, ♂: 92.5, 96; ♀: 88, 88.5. Dolphin Island, ♂: 93, 93; ♀: 87.

Though these birds are very slightly darker in colour than inland specimens (from the Canning Stock Route) of *forresti*, and perhaps slightly larger on an average, they can best be included in that race. The fresh material confirms my earlier suspicion that the type of *lewisi* was wrongly sexed and is a male, which would account for its large size.

### **Meliphaga leucotis novaenorciae** (Milligan)

The name *novaenorciae* has not generally been accepted and Milligan's (1904a) description to the contrary, I cannot detect any difference in colour between specimens from the south-west and the east of Australia, but there is a difference in size, as was correctly pointed out by Milligan (1904b). Material in the Western Australian Museum measures: New South Wales: ♂, 94 (juv.), 96,101, 102; ♀, 87, 87, 98. Victoria: ♀, 88, 92, 95; sex unknown, 92. Western Australia: ♂, 89, 91, 91, 91, 92, 94, 96; ♀, 81, 81, 82.5, 84, 85.

It is likely that the "♀" from New South Wales with a wing of 98 mm is incorrectly sexed, so that we get for the eastern states: ♂, (94), 96-102; ♀, 87-95; and for Western Australia: ♂, 89-96; ♀, 81-85. On the basis of these figures *novaenorciae* seems tenable as a form slightly smaller than the nominate race.

Notwithstanding its name, this bird has never been found at New Norcia; the Wongan Hills evidently form its western limit of distribution. Eastwards it extends at least to Zanthus (Whitlock 1922, p. 175).

### **Artamus cyanopterus** (Latham)

Keast (1958), followed by Mayr (*in* Mayr & Greenway 1962), recognised *perthi* Mathews, though as a poorly differentiated race, on the basis of having only the 2nd and 3rd primaries edged with white, while in birds from eastern Australia the 2nd, 3rd and 4th primaries show white edges. The material of this species in the Western Australian Museum shows that not only is white usually present on the 4th primary of Western Australian birds, as already indicated by Keast, but also that in eastern birds it is sometimes feebly indicated or practically absent (see table). This further weakens the case for retention of *perthi* and in my opinion the name should be synonymized. *Artamus cyanopterus* cannot be divided into subspecies.

| | 4th primary broadly edged with white | 4th primary narrowly edged with white | 4th primary amost without white |
|---|---|---|---|
| New South Wales (7 specimens) | 4 | 2 | 1 |
| Western Australia (15 specimens) | 5 | 7 | 3 |

**Cracticus nigrogularis nigrogularis** (Gould)

In a previous paper (Mees 1961, p. 126 footnote) I mentioned that birds from the extreme south-west of the Kimberley Division belong to the nominate race. The available material is the following:

| No. | Sex | Locality | Date | Wing | Bill | Weight (grams) |
|---|---|---|---|---|---|---|
| A8412 | ♂ im. | La Grange . | 28.v.1960 | 169 | 47 | 132 |
| A8413 | ♂ ad. | ,, . | ,, | 171 | 45 | 126 |
| A8415 | ♂ ad. | Leanwarringah Well (between Broome and Derby) | 30.v.1960 | 178 | 46 | 124 |
| A8414 | ♂ ad. | Derby ... . | 3.vi.1960 | 176 | 47·5 | 126 |

Two recently collected specimens from the north Kimberley Division measure:

| No. | Sex | Locality | Date | Wing | Bill | Weight (grams) |
|---|---|---|---|---|---|---|
| A8418 | ♂ im. | Kalumburu . | 26.vi.1960 | 159 | 43 | |
| A8419 | ♂ ad. | ,, ... | 24.vi 1960 | 154 | 38 | .... |

Field observations at Pardoo and Anna Plains show that the range of the nominate race is continuous along the Eighty Mile Beach. The boundary between the two races in the Kimberley Division remains to be found, but as birds from Wotjulum clearly are pure *picata*, the nominate race cannot range far into the Kimberley Division; also the boundary between the races must be rather abrupt, which suggests secondary contact. It is perhaps reasonable to assume that the nominate race has only comparatively recently worked its way up along the coastal strip of the Eighty Mile Beach. Perhaps the Kimberley specimens of the nominate race average slightly smaller than more southern birds, but they are much too large to be regarded as intermediates.

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## INSTRUCTIONS TO AUTHORS

Papers may be submitted to the Society in accordance with Rules and Regulations 38 to 41 inclusive (see below). They should be addressed to *The Honorary Secretary, Royal Society of Western Australia, Western Australian Museum, Perth.*

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38. Every paper intended to be read before the Society or to be published in the Society's Journal must be sent to the Secretaries at least seven days before the date of the next ensuing Council meeting, to be laid before the Council. It will be the duty of the Council to decide whether such contribution shall be accepted, and if so, whether it shall be read in full, in abstract, or taken as read. All papers accepted for publication must be read or otherwise communicated at an ordinary meeting prior to publication.

39. A Publications Committee, appointed by the Council, shall recommend to the Council whether a paper presented to the Society shall be published in the Society's Journal. The Publications Committee may obtain an opinion from any person it may select on the suitability of any paper for publication.

40. Publication in the Society's Journal shall only be available to *(a)* Ordinary Members, *(b)* Honorary Members, *(c)* Non-members resident outside Western Australia, who must communicate the paper through an Ordinary or Honorary Member. No paper shall be accepted from a Non-member resident in Western Australia.

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# Journal

# of the

# Royal Society of Western Australia

Volume 47 1964

Part 3

## Contents

10.—Notes on the Skulls of Two Western Australian Rodents with a key to the Skulls of the Rodents of Southwestern Australia. By Ernest Lundelius, Jr.

11.—Effects of Salt, Temperature and Seed Scarification on Germination of Two Varieties of Arthrocnemum halocnemoides. By C. V. Malcolm.

12.—Ashbed and Nutrients in the Growth of Seedlings of Karri (Eucalyptus diversicolor F. v. M.). By O. W. Loneragan and J. F. Loneragan.

13.—Foraminiferal Evidence for the Paleocene Age of the King's Park Shale (Perth Basin, Western Australia). By Brian McGowran.

14.—Projasus—a New Generic Name for Parker's Crayfish, Jasus parkeri Stebbing (Palinuridae: "Silentes"). By R. W. George and J. R. Grindley.

Memorial—Douglas Elwood White.

15.—Geographical Variation and Distribution of some Birds from Western Australia. By G. F. Mees.

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JOURNAL OF

# THE ROYAL SOCIETY

OF

# WESTERN AUSTRALIA

VOLUME 47 (1964)

85977/7/64—570

# Annual Report of the Council of The Royal Society of Western Australia for the Year ending 30th June, 1963

### Membership

There are 246 members on the register of the Society. They are as follows:—

| | |
|---|---|
| Honorary | 1 |
| Life | 3 |
| Corresponding | 2 |
| Ordinary | 212 |
| Associate | 14 |
| Student | 14 |

In the past year 14 Ordinary and 1 Student Members were elected. Four Ordinary Members resigned.

It is with regret that we record the deaths of two Honorary Life Members, Mr. Ludwig Glauert and Miss Enid Allum. Mr. Glauert, a foundation member, served on Council for many years and was President for two years. He received the Kelvin Medal from the Society in 1945. Miss Allum joined the Society in 1915, and served as Treasurer for many years.

### Council

Eleven Council meetings were held at the Zoology Department of the University in the past financial year. Attendances were as follows:—

Dr. W. D. L. Ride 8, Professor R. T. Prider 10, Dr. N. H. Brittan 7, Dr. R. W. George 5, Dr. J. E. Glover 10, Dr. L. W. Samuel 11, Mr. C. F. H. Jenkins 7, Mr. J. G. Kay 7, Mr. R. J. Little 9, Mr. C. V. Malcolm 6, Mr. D. Merrilees 7, Mrs. A. Neumann 9, Mr. P. Pillow 11, Miss M. E. Redman 11, Mr. R. D. Royce 8, Mr. W. R. Wallace 8.

### Publications

The Editor, Dr. Glover, maintained the high standard of the Journal in the publication of volume 45, parts 2, 3 and 4 and volume 46, part 1. Mr. Royce and Dr. Mees assisted with the distribution and editing.

The Proceedings, compiled by Mr. Malcolm, appeared regularly with notices of General Meetings, summaries of previous Meetings, and items of general interest to members.

### Library

The Librarian, Mrs. Neumann, has catalogued all holdings, revised the entries for the C.S.I.R.O. List of Scientific Serials and reviewed the exchange list. Although £60 was spent on binding, there remains a considerable amount to be done.

New exchanges were arranged with six institutions: Institute of Caribbean Studies of the University of Puerto Rico; University College of Addis Ababa, Ethiopia; Academy of Science of the Kazakh S.S.R., Alma Ata; Deutsche Akademie der Wissenschaften zu Berlin, Germany; Institute of Geology, University of Parana, Brazil; Naturwissenschaftlicher Verein für Steiermark, Graz, Austria. The total number of exchanges is now 217.

### General

The Standing Committee on Conservation, which was appointed by Council to advise on matters involving the preservation of Western Australian flora, fauna and geological features, has beeen active. The members are Mr. C. F. Jenkins (President), Professor B. J. Grieve, Drs. A. R. Main, P. E. Playford, W. D. L. Ride and D. Serventy, and Messrs. G. E. Brockway, T. Cleave, A. J. Fraser, J. F. Morgan and R. D. Royce.

During the year, two films were shown and seventeen papers and talks were given. They were entitled as follows:—

"Symposium on flies", by C. F. H. Jenkins, Dr. D. R. R. Snow and Dr. A. Zorbas.
"The pebble crabs of W.A.", by Dr. R. W. George.
"The life cycle of the plant pathogen *Sclerotina sclerotiorum* in W.A.", by R. M. Henderson, presented by Mrs. E. R. L. Johnson.
"The foraminifera of Oyster Harbour, W.A.", by K. McKenzie.
"Some aspects of forestry in Africa", by W. R. Wallace.
"Cave paintings of the West Kimberley", by Dr. P. E. Playford.
"Botanic gardening", by Dr. M. Phillips.
"Seismicity of Western Australia", by I. B. Everingham.
"Fossil mammals of the Nullabor caves", by Dr. E. Lundelius, presented by Dr. W. D. L. Ride.
"Evolution in Isotoma", by S. James.
"Development of the South Perth Zoo", by C. F. H. Jenkins.
"Fossil coastline of Geographe Bay, near Capel, W.A.", by J. G. Kay.
"Behaviour and physiological studies of lizards", by W. R. Dawson, P. Licht, S. D. Bradshaw and V. Shoemaker.
"Symposium on conservation", by Drs. W. D. L. Ride, A. R. Main and P. E. Playford and Mr. R. D. Royce.
"Honey and beeswax production in Tanganyika", by Dr. F. G. Smith.
"The gekkonid genus *Nephrurus* in Western Australia", by Dr. G. Storr.
"Agricultural prospects of the Forrestania area", by G. H. Burvill.

In conclusion, the Society would like to record its thanks to the State Treasury for its continued support of the publication of the Journal, to the Government Printer for his co-operation in the Journal publication, and to the Museum Board for the housing of the library and for providing premises in which to hold the regular meetings.

W. D. L. RIDE,
*President.*

M. E. REDMAN,
*Joint Hon. Secretary.*

Journal
of the
Royal Society of Western Australia

Vol. 47 Part 4

# 16.—A Review of Australian Fossil Marsupials

## Presidential Address, 1963

By W. D. L. Ride, M.A., D.Phil.*

*Delivered—15th July, 1963*

## Contents

Page
Classification .... 98
Phylogeny .... 100
Marsupicarnivora .... 101
  Australian Marsupicarnivora .... 103
  Thylacinidae .... 105
  Dasyuridae .... 109
    *Glaucodon ballaratensis* .... 110
    *Dasyurus affinis* and *D. bowlingi* .... 111
    *Sarcophilus laniarius* and *S. prior* .... 111
  Myrmecobiinae .... 111
Peramelina .... 112
  *Ischnodon australis* .... 112
Diprotodonta .... 112
  Wynyardiidae : *Wynyardia bassiana* .... 114
  Phalangeridae .... 115
    *Perikoala palankarinnica* .... 118
    *Burramys parvus* .... 118
  Macropodidae .... 119
    Generic Classification .... 119
    Structure and Terminology .... 121
    Phyletic lines .... 123
  The Grange Burn potoroo .... 123
  Diprotodontidae .... 125
  Vombatidae .... 125
*incertae sedis* : Notoryctidae .... 125
The Australian Radiation : Origin, Isolation and Drift .... 126
Appendix : Statistical Determination of Subspecies 128
References .... 129

## Introduction

In recent years there has been a great resurgence of interest in Australian marsupials. In the case of the modern mammals this has produced a vast body of information through the application of modern physiological and ecological techniques, knowledge which is now replacing the natural history anecdotes and zoological inferences of past generations. In a similar fashion, the advent of the four-wheel drive vehicle, of plastics, and the discovery of new techniques for handling data, have produced encouraging signs that knowledge of fossil marsupials is also likely to increase. Today, palæontological field-work aimed at the discovery of new fossil marsupials in Australia is going on from most of the Australian museums and also, with spectacular success, from several American universities. Unfortunately, as yet, only a small fraction of the results of this new work has been published.

Despite our present-day activity and the publications of our predecessors, our knowledge of pre-Pleistocene marsupials remains small because descriptions are, as yet, available of only very few Tertiary fossils and of these only one (*Wynyardia*) is certainly older than Miocene. Preliminary descriptions have been published of some of the recently discovered middle and upper Tertiary forms from Central Australia (Stirton 1955, 1957a), while stratigraphic information from a number of sources is also being made available (Stirton, Tedford & Miller 1961, Ludbrook 1963, 1963a, Balme 1963). When the full descriptions, proper comparisons, and the ages of these fossils are known they will provide the first real framework for palæontological studies on the Age of Marsupials in Australia.

Although there are great numbers of Pleistocene fossil marsupials in the Australian Museums, little has been done with them since they were originally described. Thus, advances in the knowledge of the anatomy and classification of recent forms, and concepts of population biology and of faunistics, have played little part in their interpretation. In addition, most of the early workers did not recognise the need for accurate stratigraphic localization. Thus, it is scarcely surprising that one of the most pressing tasks in Australian Palæontology today is that of rediscovering the classic localities, and localizing the old material through comparison with new It is only in this way that the species names in use can be stratigraphically allocated, and it is only through these new collections that ranges of morphological variation of the various species will be determined. At present "species" are often represented by samples which may not be stratigraphically homogeneous and population studies based upon them may be quite erroneous. An outstanding example of such work has been the studies of Woods (1960a), and more recently of Bartholomai (1962, 1963), on the Darling Downs faunas. Woods has shown that this material, which was formerly regarded as a single rather mixed unit, belongs to two distinct

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* Western Australian Museum, Beaufort Street, Perth.

successional faunas. Although physical superposition has not yet been demonstrated, these are probably Upper Pliocene and Lower (or Mid) Pleistocene.

Such work, if it is to be done to modern standards, is very slow and it is fortunate that (even omitting the numbers of overseas workers) there are in Australia today almost as many active researchers in this field as there have been in the whole of our history.

The review which I present here is a general one of the outlines of our knowledge of Australian fossil marsupials to date. However, in it I also take the opportunity to give fresh data and conclusions relative to a number of fossils which I have studied but have not yet published upon. These are *Glaucodon ballaratensis*, the *Thylacinus* complex, the Grange Burn "cuscus" (which is not a cuscus but a potoroo), and *Wynyardia bassiana*. I also propose a new ordinal classification of the Marsupialia to bring their arrangement more into line with that accepted for the Eutheria. I also consider the current status of the Continental Drift hypothesis and conclude that it provides an adequate explanation for anomalies in the composition of the Australian mammalian fauna.

### Classification

Today, marsupials occurring in Australia are usually classified into three major groups. These, following Simpson's (1930) example, are conventionally given the rank of Superfamilies, as are the three other major taxa of marsupials which occur in Palæarctic and Neotropical regions (*see* also Simpson 1945). This rather low rank for each of these groups fits well with the traditional practice of regarding the Marsupialia as a single Order of Mammalia, but it also implies an unwarranted degree of homogeneity in a group of animals which have evolved for just as long as the Eutheria have; by contrast these are currently subdivided into twenty-six Orders.

Fossil marsupials, particularly those of the Australian Pleistocene, clearly demonstrate a wide variety of forms which, if they had been eutherian, would have been distributed among several orders. Thus, if the kangaroos and wallabies are antelope- and deer-like, the sthenurines bovid-like and the diprotodontids hippo-like then the native cats can only represent some such unspecialized Carnivora as the civets and mongooses. The bandicoots are very different again from both of these groups and clearly invite comparison with yet another order.

This idea is not anything original for taxonomists have long recognized this inconsistency in classification. For example, Cain (1959, p. 214) has said in explanation: "Because of their peculiar features [marsupials] are always ranked as a single order of mammals within a separate class, although the briefest inspection is enough to show that there is at least as much difference between a kangaroo and a dasyure (for example) as between an insectivore and a rodent, let alone a rodent and a lagomorph. Because eutherian mammals were the first to become familiar to the anatomists of the western world, and even more because our species belongs to them, they have been taken as normal and the extraordinary 'abnormality' of the marsupial urinogenital system has sufficed to keep marsupials as a single order. Had we known the marsupials first and especially if we had belonged to them, they would have been classified in several orders, and no doubt the 'abnormality' of the eutherian genitalia would have sufficed to keep the number of eutherian orders much lower than at present."

In the classification which follows I do not discard the six superfamilies but, in order to emphasize the breadth of the whole radiation, and since I believe that a synthetic view of palæontology and neontology requires it, I group these further.

In an earlier review of the beginnings of the marsupials and of the main features of their phylogeny (Ride 1962) I had pointed out that marsupials had formerly been grouped in two higher taxa (suborders) and the abandonment of these by Simpson in 1930 was one of the most important advances in marsupial classification of our time. Through discarding them Simpson promoted a freer mental approach to problems of interrelationship within the marsupials as a whole. The problem which now arises is whether or not a new ordinal classification would have the same restrictive effect as did the subordinal classifications attributed to Owen and Bensley (or de Blainville). I think that this is unlikely because it cuts across no phylogenetic divisions It also raises no problems of intercontinental migration.

The earlier classifications raised problems in both of these directions.

Although Owen's classification into Polyprotodontia and Diprotodontia was not intended to be phylogenetic it became so in the minds of students and, when the cænolestoids were added to the Diprotodontia, argument inevitably became confused with the issue of Continental Drift. By constrast, Bensley's classification was phylogenetic but was complicated by his misinterpretation of the structure of the didelphoid foot (*see* Goodrich 1935), but better understanding today makes it possible that his Syndactyla will eventually be used as a "cohort" in future marsupial classifications. Both systems (as phylogenetic arrangements) had their proponents and the problems in the minds of students as to which was more likely to be correct were only disposed of by Simpson's action in abandoning them altogether. He rejected these "key-classifications" which were based on single characters and subdivided the Marsupialia into five or six groups of very different importance and variety but of equal or nearly equal antiquity.

In 1930 there seemed to be no good reason for grouping the superfamilies into taxa at higher level but, since then, fossils of about the right age (Palaeocene and Lower Eocene) and with suitable characters to provide a transitional stage between the non-Australian superfamilies Didelphoidea and Borhyaenoidea have been discovered (i.e. *Eobrasilia* Simpson 1947 and *Patene*-like forms Simpson 1948, p. 49). If the Dasyuroidea be added to these—and there is little to argue against this course in spite of the absence of transitional fossils between them and the South American superfamilies—then the argument that Dasyuroidea, Didelphoidea and Borhyaenoidea form a single unit comparable with the eutherian Carnivora becomes even stronger. Most authors regard the modern Dasyuroidea as not very greatly modified descendants of the original didelphoid invaders of Australia and, since the Phalangeroidea at least (and also the Perameloidea) warrant ordinal status by comparison with Eutheria, I take the formal step of proposing four orders of Marsupialia.

The classification which I adopt is as follows:

Class MAMMALIA Linnaeus, 1758.
Infraclass METATHERIA Huxley, 1880.
Superorder MARSUPIALIA Illiger, 1811.

Order 1. MARSUPICARNIVORA *nov.*

Superfamilies

1. Didelphoidea : American Opossums etc., U. Cret—L. Mioc, Pleist—R, N. Amer.; Eoc-Mioc, Western Europe; Palaeoc—R, S. Amer.
2. ‡Borhyaenoidea : South American marsupial carnivores. Palaeoc-Plioc, S. Amer.
3. Dasyuroidea : Australian Native-cats etc. ?Mioc — R, Aust.; R, N. Guinea.

   Families

   1. Dasyuridae : ?Mioc — R, Aust.; R, N. Guinea.
   2. Thylacinidae : U. Plioc — R, Aust.; ?Pleist, N. Guinea.

Order 2. PAUCITUBERCULATA* Ameghino, 1894.

Families

1. Caenolestidae : Oppossum rats etc., Palaeoc — R, S. Amer.
2. ‡Polydolopidae : Palaeoc — Eoc, S. Amer.

Order 3. PERAMELINA Gray, 1825.

Family

1. Peramelidae : Bandicoots, Plioc — R, Australia; R, N. Guinea.

Order 4. DIPROTODONTA Owen, 1866.

Families

1. Phalangeridae : Possums, cuscuses, marsupial lions, etc., ?Mioc — R, Aust.; R, N. Guinea.
2. ‡Wynyardiidae : Oligocene, Tasmania.
3. Vombatidae : Wombats. Pleist — R, Aust.
4. ‡Diprotodontidae : Mioc — R, Aust.; ?Plioc, N. Guinea.
5. Macropodidae : ?Mioc — R, Aust.; ?Plioc — R, N. Guinea.

Marsupialia *incertae sedis*

Family Notoryctidae : Marsupial Moles. R, Aust.

*Numbers of genera in orders.*—If the fossil and modern genera of these orders are counted and the generic concepts of a single conservative author are employed (G. G. Simpson 1945), they fall well within the range of magnitude of orders of Eutheria. Thus:

Marsupialia — Marsupicarnivora 64, Paucituberculata 21, Peramelina 5, Diprotodonta 48. *Incertae sedis* 1.

Eutheria (some orders only) — Embrithopoda 1, Tubulidentata 1 (possibly 2§), Dermoptera 3, Pholidota 1 (possibly 4§), Pyrotheria 4 (possibly 6§), Dinocerata 8, Astrapotheria 9, Hyracoidea 13, Sirenia 16, Proboscidea 24, Lagomorpha 33, Perissodactyla 158, Carnivora 377, Artiodactyla 419.

In making these comparisons, however, we must remember that we know little of the fossils of some of these marsupial orders and the values shown here for the numbers of genera included in each are not really comparable with those given for the eutherian orders because they are too low. This is made clear by comparing the approximate percentages of genera of marsupial and eutherian orders which are known only as fossils. Since a number of the smaller orders of Eutheria are known only as fossils, comparison has been limited here to those which, like the orders of Marsupialia, contain some living representatives. The percentages of genera known from fossils only in each order are:

Marsupialia — Marsupicarnivora 68%, Peramelina 0% Paucituberculata 86%, Diprotodonta 35%.

Eutheria — Tubulidentata possibly 50%§, Dermoptera 67%, Pholidota possibly 75%§, Hyracoidea 77%, Sirenia 88%, Proboscidea 92%, Lagomorpha 70%, Perissodactyla 96%, Carnivora 70%, Artiodactyla 80%.

The same data reveal that our knowledge of non-Australian fossil marsupials is comparable with that of eutherians but knowledge of the Australian forms lags far behind that of eutherian orders of comparable size. This is emphasized by the removal of the Australian component from Marsupicarnivora; this causes the value to rise to 80%, with 0% of purely fossil genera known within the Dasyuroidea||.

The marsupial orders do not match the eutherian orders only in numbers of genera but also in the breadth of their adaptive radiations. I have already made brief mention of similarities between Diprotodonta and Artiodactyla and, in general outline, a similar comparison can be drawn between Marsupicarnivora and Carnivora. In making such a comparison it must be first recognized that the total adaptive scope of the two orders is not directly overlapping. Thus, some ecological branches (like the Pinnipedia and some wholly vegetarian Procyonidae) of the

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* I follow Cabrera 1919 in adopting Ameghino's name for this taxon and like him exclude *Microlestes* and *Hypsiprynopsis* from the concept as well as the "Hypsiprymnoidea"—see Ameghino 1903 (Vol. 13, p. 962 of *Obras completas*).

‡ taxa comprising extinct forms only.

§ Figures qualified thus are obtained by including those genera which Simpson includes with reservation.

|| In these figures *Glaucodon* (Dasyuroidea) and *Ischnodon* (Peramelina) are not included because they were published after the date of Simpson's 1945 monograph from which the data are drawn. To insert these without adding newly described genera of Eutheria would be pointless.

radiation of Carnivora are missing from Marsupicarnivora, but the Marsupicarnivora is widened in other directions through including many of the equivalents of the eutherian order Insectivora within it; these are excluded from Carnivora. Otherwise, remarkable similarities exist between the taxa. Relatively unspecialized carnivores approaching Mustelidae and Viverridae are found in Borhyaenoidae (*Amphiproviverra*) and Dasyuroidea (*Dasyurus*), and omnivorous animals like the marsupials *Didelphis* and *Philander* can be equated with members of the Raccoon family (Procyonidae, e.g. *Bassariscus*). *Sarcophilus*, the Tasmanian Devil, is like a Wolverine (*Gulo*) or a Hyaena in its carnivorous specializations and *Thylacinus* is like a wolf. *Chironectes* (the Water Opossum) with its slightly flattened tail and webbed toes might even be regarded as an early approach to otter-like form. One of the most remarkable ecological and functional similarities is that between *Thylacosmilus* the Marsupial Sabre-tooth (Pliocene, South America) and *Smilodon* and the other true sabre-tooth tigers (see Simpson 1941a). As far as I know there is no direct equivalent between marsupials and such highly specialized herbivorous carnivores as the procyonids *Potos* (the Kinkajou) and *Ailuropoda* (the Giant Panda) but, as already mentioned, this is only to be expected when broad comparisons are being drawn between orders.

The insectivore-like forms among the Marsupicarnivora include Didelphoidea: *Peratherium*, Eocene-Miocene Europe, North America; *Marmosa**, mouse-opossums, Recent South America; and Dasyuroidea: *Sminthopsis*, *Planigale* and *Antechinus*, Marsupial-mice, Recent and Pleistocene, Australia. Some of these are arboreal, e.g. *Marmosa* and *Caluromys* of South America, and *Phascogale* (*sens. strict.*) of Australia. This latter genus should possibly be equated with the tree-shrews *Tupaia*. If *Notoryctes* (the Marsupial Mole) should prove to be a dasyuroid its only equivalent is also in the Insectivora (i.e. *Talpa* or *Chrysochloris*).

Finally, the taxa have comparable ranges in time: Carnivora occurred from the L. Palaeocene to Recent, and Marsupicarnivora from the U. Cretaceous to Recent.

## PHYLOGENY

Lacking fossils we can only derive the probable relationships of the Australian marsupial orders by inference from the characters of their modern representatives. Such a phylogenetic tree is shown in fig. 1. This is essentially the same as that shown in my 1959 review of some problems of marsupial phylogeny (Ride 1962) but incorporates the ordinal classification given here. It illustrates the conclusion that the major groups of marsupials may be arranged as a series of structural grades. Recently Masai (1960) and Dillon (1963) have published results which threw some doubt on the position at which duplicicommissuraly (i.e. the possession of a fasciculus aberrans in the forebrain) should first appear in this dendrogram. Their results are so at variance with those of earlier workers, such as Elliot Smith and A. A. Abbie, that I have not taken them into account and it is quite clear that further examination of specimens of the various species must be made in case the apparent disagreement is produced by differences in technique, in interpretation, or even through faulty material.

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* Information on the dietary preferences of South American mammals referred to in this review is from Hall & Dalquest 1963.

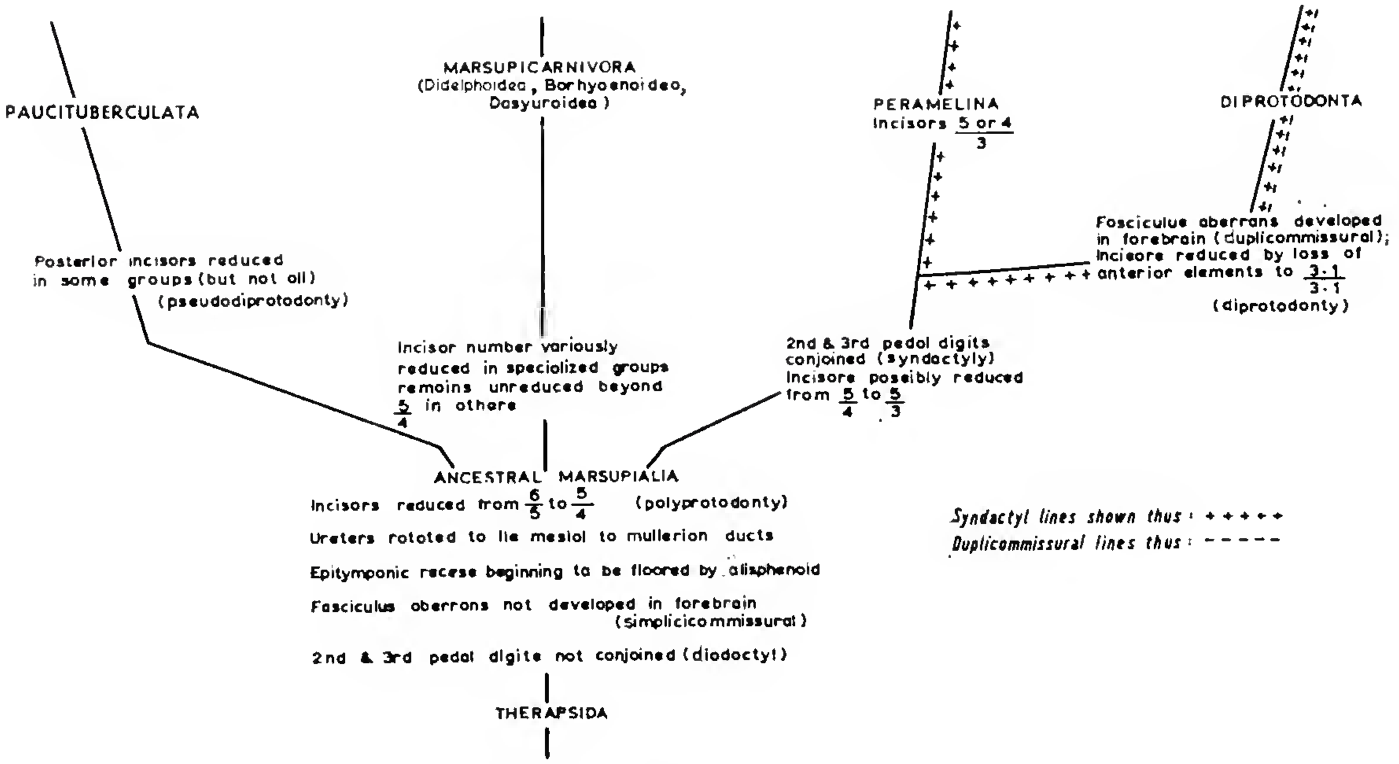

Fig. 1.—The sequence of morphological differentiation in the evolution of marsupial orders (modified from Ride 1962).

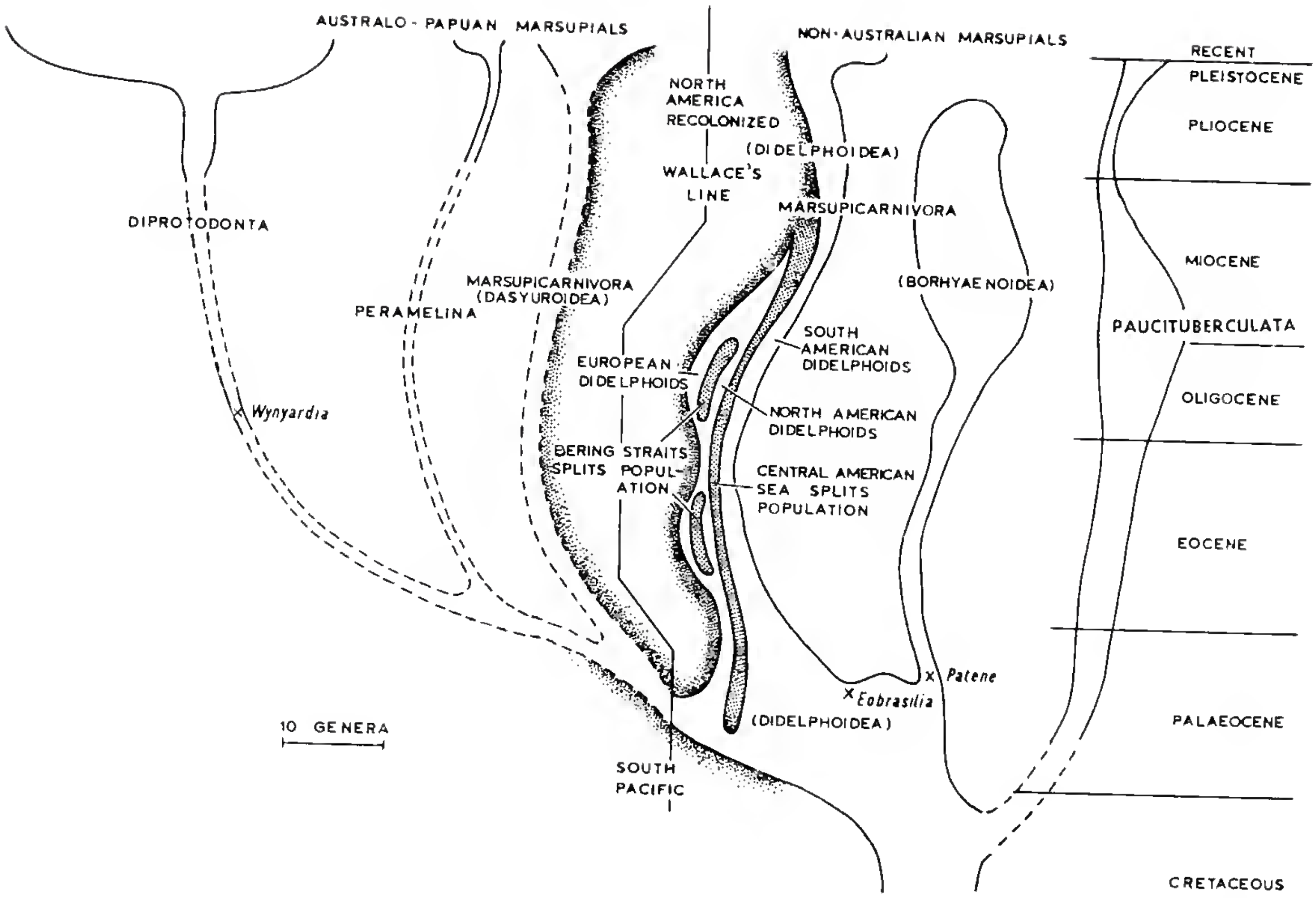

Fig. 2.—A family tree of marsupials. Horizontal distances between unbroken lines limiting phyla represent known numbers of genera. Stipple represents aquatic barriers (modified from Ride 1962).

If the results of Masai and Dillon were to be confirmed, they would produce no change in the general phyletic outline but they would have the result of pushing the evolutionary origin of the fasciculus aberrans into the various lines within the already evolved Diprotodonta, since some of these will be like all other marsupials in lacking it while most will possess it. However, Masai states that some Diprotodonta posses a corpus callosum. If this is so, they differ from all other marsupials and resemble Eutheria—a somewhat remarkable state of affairs.

The widely held view of the fundamental dichotomy between marsupial and eutherian female urinogenital systems has been challenged by Kean (1961). He holds that the median (eutherian) vagina has become reduced in the marsupial line, following the reduction in size of the neonatus, and lateral vaginae have evolved as neomorph seminal ducts. It is Kean's view that embryological evidence is equivocal.

Figure 2 is a graphic summary of geographical and temporal distributions combined with the dendrogam of Fig. 1. Horizontal breadths of the ascending phyla represent the known numbers of genera at each horizon, and the diagram gives some indication of marine barriers to dispersal. However, it takes no account of the possible role of the Tethys sea as a barrier to dispersal from northern to southern Eurasia and leaves the question unanswered as to whether marsupials entered Australia by means of a southern intercontinental connection or across Wallace's Line.

## MARSUPICARNIVORA

The fossil evidence of relationship between the two main groups of American Marsupicarnivora (the Didelphoidea and Borhyaenoidea) lies in the fossils *Eobrasilia*, *Patene* and a problematical group of five isolated molars of which Simpson (1948, p. 49) says: "These various teeth appear to represent a morphological group of fairly unified nature and intermediate in its (admittedly too few) known characters between borhyaenids and didelphids. The isolated teeth could be referred to either family. Among the Borhyaenidae they would be the most primitive known forms, among the Didelphidae the most advanced in the borhyaenid (or predaceous) direction. On the whole, I think them somewhat closer to borhyaenids, but they are almost perfectly intermediate as far as they go. In conjunction with the almost equally primitive *Patene*, they give a clue, slender but real, to the ancestry of the Borhyaenidae."

Simpson sums up his attitude (1948, p. 40) to the relationship of didelphoids, dasyuroids and borhyaenids by saying: "Traced as far as possible to its fundamentals, the structure of borhyaenids in general seems clearly derivable from a primitive stock certainly pre-thylacinid and comparable only to the didelphids and the most primitive dasyurids. It resembles both these stocks (which are very similar in essentials), and there is no conclusive evidence of relations to one or the other. Adaptively the group parallels the dasyuroids, but its inferred structural ancestry appears rather more didelphoid. The most probable conclusion is that in the Upper Cretaceous the didelphoids and dasyuroids had a common ancestry sharing the primitive characters of both groups, somewhat more like the Didelphidae than the Dasyuridae as we know them because the former are more conservative. From this stock the borhyaenids arose. They may very well have arisen from a carnivorous line progressing in the direction of the Dasyuridae, but not very far along this line, and surely before it had acquired its most characteristic specializations."

Of course, there are no fossil intermediates between dasyuroids and the American forms but comparison of the characters of even modern Dasyuroidea with Didelphoidea and Borhyaenoidea reveal no differences which separate them unequivocally.

Modern dasyuroids differ principally from didelphoids in that they are specialized in a carnivorous (or insectivorous) predaceous direction and are primarily cursorial. Thus Dasyuridae seldom possess the opposable hallux of the scansorial didelphoids and in this they resemble some Borhyaenidae (see *Prothylacinus* in Sinclair 1906, p. 371 and pl. 54) but not all. Whether the dasyuroid foot with its small and non-fully-opposable (and often very reduced) hallux and its frequently high degree of terrestrial specialization is more primitive than the highly specialized arboreal form of the didelphoid foot is not known. I know of no description of the hallux of a mesozoic mammal and I consider that Bensley's (1903, p. 163) view that the terrestrial foot of dasyuroid marsupials is secondly derived from the arboreal one is no more than an assumption. Bensley's belief is derived from Dollo's statements (1899, 1900) and from Bensley's own observation (p. 191) that the didelphoid *Marmosa*, which has an opposable hallux, meets the requirements of a prototype for the entire Australia marsupial radiation because it possesses "an indication of the syndactylous condition of the Phalangeridae". His conviction that this approach to *Marmosa* was reasonable was strengthened for him by the presence of the "primitive" five external stylar cusps on the upper molars of the same genus. Goodrich (1935) has shown that his statement regarding syndactyly in *Marmosa* is erroneous. Bensley also pointed out that the dasyuroids differ from didelphoids in incisor number; dasyuroids never possessing more than 4/3. However, this statement is only true in relation to modern didelphoids since some (e.g. *Eodelphis cutleri*, Cretaceous, Belly River Fm., Canada. Simpson 1929, p. 128) have also reduced their lower incisors to three. Borhyaenidae reduce their lower incisors even further; thus *Borhyaena excavata* and *B. tuberculata* have an incisor formula of 3/2 while *Thylacosmilus* possesses none at all.

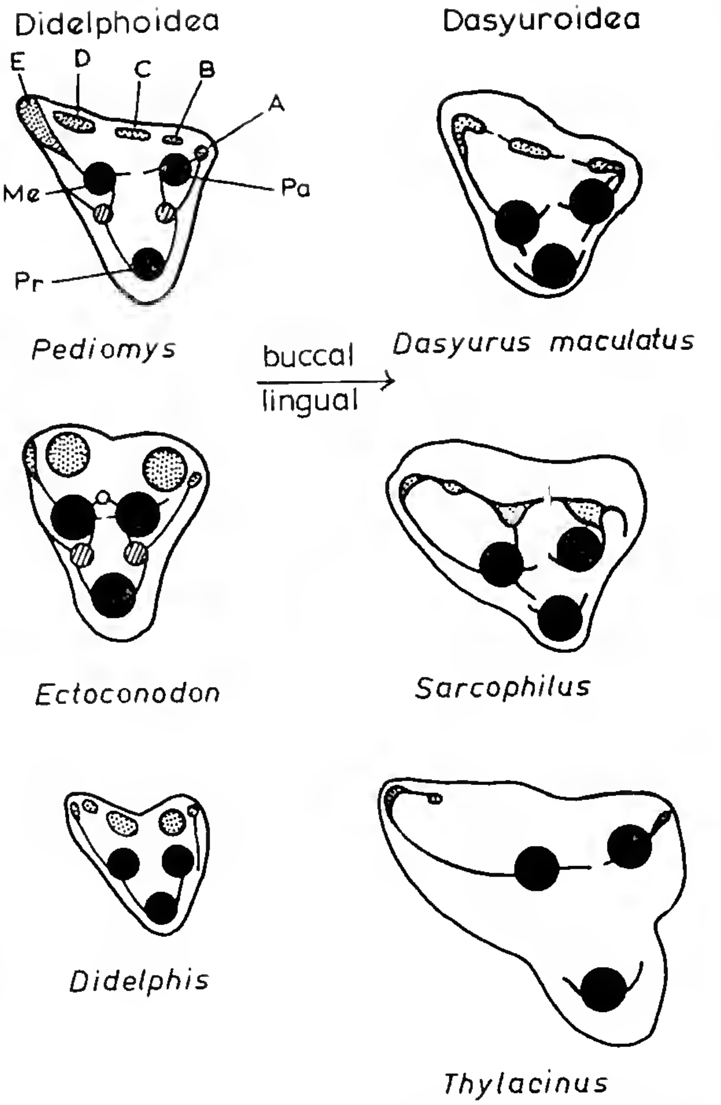

Fig. 3.—The cusps (black circles) and stylar cusps (stipple) of the upper molars of Didelphoidea and Dasyuroidea. (Didelphoids after Simpson 1929, p. 119; dasyuroid second upper molars in collection W. Aust. Mus.)

The molars of most modern dasyuroids differ from those of most didelphoids in that they lack the full complement of external stylar cusps which Simpson has shown (from a study of very numerous Cretaceous didelphid upper molars as well as that of a large series of later didelphids from all known horizons; Simpson 1929, p. 119) is ancestral in the Didelphoidea—see fig. 3. These cusps vary considerably but Simpson says that, in teeth of the didelphid type, stylar cusp A is always present and is only slightly external to the paracone save on $M^4$. B is never well developed, while C and D are about equally developed and usually form ridge-like crests parallel to the outer border. E is always present except on $M^4$. In modern Dasyuroidea there are seldom more than three stylar cusps present. However, in Borhyaenoidea although the earliest forms possess the full complement of stylar cusps (e.g. the five *Patene*-like molars illustrated in Simpson 1948, p. 49) more specialized forms have progressively fewer, *Patene* and *Procladosictis* (Palaeocene and Eocene) having only twin styles opposite the paracone and metacone and *Amphiproviverra*, *Prothylacinus* and *Borhyaena* (Miocene) having only a single anteroexternal stylar cusp (Sinclair 1906). In *Thylacosmilus* (Pliocene) they are absent (Simpson 1941). The lack of a full complement of stylar cusps can thus scarcely be said to be a dasyurid character.

It is unfortunate that very little detailed descriptive comparative work has been published on the epitympanic region of marsupials since it seems likely that this structure may prove to be a better indication of separate phyletic lines in the Marsupicarnivora than the dentition. In Dasyuridae the epitympanic sinus anterior to the epitympanic recess is always ventrally enclosed in an alisphenoid bulla which grips the tympanic ring laterally (fig. 4). It is widely open into the epitympanic recess posteriorly. The dorsal and anterolateral part of the epitympanic sinus is also greatly excavated into the substance of the alisphenoid and the squamosal where it may even penetrate into the root of the zygomatic arch dorsal to the glenoid. While the ear of *Thylacinus* is superficially rather different in appearance with its small flattened, and posteriorly incomplete, bulla and dorsally situated epitympanic sinuses, it is clearly derivable from that of the more typical dasyurid condition. In *Didelphis* (and in *Wynyardia* see p. 115) there is no dorsal or anterolateral "excavation" and the cavity (which probably represents the epitympanic recess alone) is only partly floored by an incomplete tympanic (or bullar) wing of the alisphenoid. Since the marsupials alone floor the epitympanic recess with the alisphenoid (Ride 1962) the uncomplicated condition seen in *Didelphis* is more likely to be primitive than the fully enclosed and "excavated" condition of Dasyurinae. Simpson's (1929, p. 129) illustration of the glenoid region of the Cretaceous didelphoid *Eodelphis*, while very incomplete, suggests a condition similar to that of *Didelphis*: the illustrations of Borhyaenoidea by Sinclair (1906) show yet another condition which may indicate that the structure will be useful in phylogenetic studies.

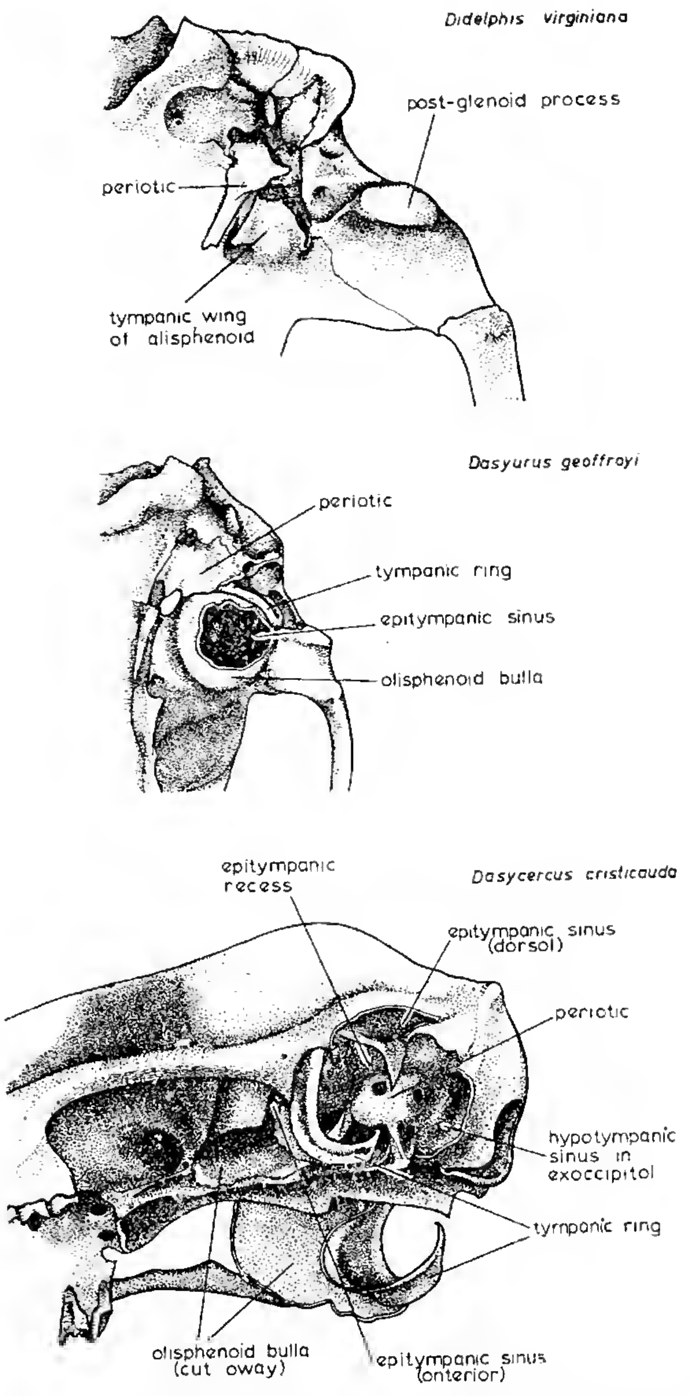

Fig. 4.—The epitympanic region of Marsupicarnivora. In both dasyuroids the alisphenoid bulla is cut away to reveal the epitympanic sinus. In *Dasycercus cristicauda* the squamosal and exoccipital are also cut away. The tympanic ring of the specimen of *Didelphis* has been lost. (Specimens in W. Aust. Mus.)

It seems that proper study of the Marsupicarnivora will reveal distinct lineages coming from a single basal stock but because Dasyuroidea on the one hand and Didelphoidea and Borhyaenoidea on the other are not far separate and subject to very similar pressures, and have been given equal ecological opportunities, a commonly-held mosaic of characters will persist giving rise to many examples of pairs of species in these different phyletic lines: pairs which more closely resemble each other than they do their less distantly separated relatives within their own lines. An example of this sort may well be the very strong resemblance between *Thylacinus* and Miocene Borhyaenidae, and it is probably also the reason for the result obtained by Wood (1924) who, when he compared forty-nine characters of Miocene Borhyaenidae, modern Dasyuroidea (including *Thylacinus*) and modern Didelphoidea, only obtained one "character" which unequivocally separated Dasyuroidea from the rest combined. This "character" was the location of dasyuroids in Australia while the other two superfamilies were confined to the Old World and the Americas (seventeen characters separated Didelphoidea from the other two, while five separated Borhyaenidae).

## Australian Marsupicarnivora

### Superfamily Dasyuroidea

The native cats and their allies are a complex group. They are entirely Australo-Papuan and exhibit all grades of carnivorous specialization from those of the eaters of very small prey (e.g., insects and other arthropods, small mice and birds) like *Planigale* and *Sminthopsis* to those of highly specialized mammal killers and carrion feeders like *Sarcophilus* and *Thylacinus*. The transformation through the degrees of carnivorous specialization in normal members of the family takes place without reference to generic distinction and is closely connected with increase in the size of the body (Bensley 1903, p. 91). Among Dasyuroidea there are highly specialized forms which have become so modified that their immediate relationships are unknown. These are *Thylacinus*, the Tasmanian Wolf and *Myrmecobius* the Banded-anteater (termite-eater). These two genera are usually placed in separate major taxa from the others in a non-committal fashion; I employ Myrmecobiinae and Thylacinidae here in this manner. Their relative status as subfamily and family is entirely artificial and is adopted because, subjectively, the specializations of *Myrmecobius* for termite eating are more understandable as a development of typical dasyuroid structure than the obviously widely divergent yet parallel carnivorous specializations of *Thylacinus* which contrast strongly with those of *Sarcophilus* and other Dasyuridae. These paral-

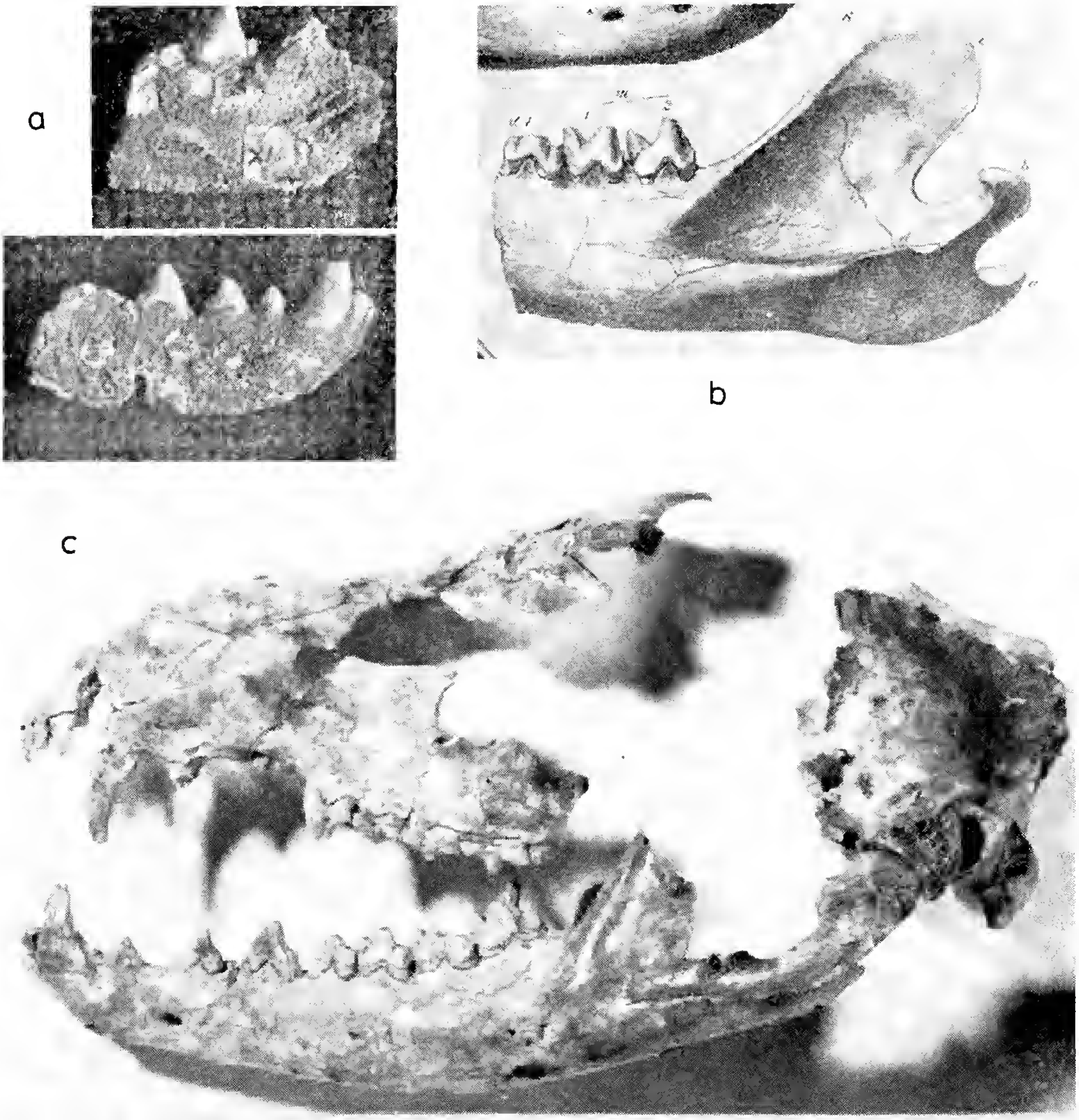

Fig. 5.—Type specimens of fossil *Thylacinus*. (a) Syntypes of *T. spelaeus* (Owen); Brit. Mus. (N.H.) Nos. Geol M10800, M10801. (b) *T. major* Owen; specimen unknown—fig. from Owen. (c) *T. rostralis* De Vis; Qd. Mus. No F 730 (photograph by courtesy Qd Mus.). (a) and (c) to same scale; scale of (b) unknown.

lel specializations probably reveal an early divergence of two predaceous phyla within Dasyuroidea.

It might even be reasonable to give the Thylacinidae superfamily rank and regard their relationship to Dasyuroidea as being the same as that between Didelphoidea and Borhyaenoidea. However, to date, only one genus and probably only one species is known and it seems best to leave things as they are until further material shows that the lineage of *Thylacinus* is as old and as diverse as that of the Borhyaenoidea. Stirton *et al* (1961) suggest that a specimen from the Etadunna Formation of central Australia (?Mioc, Ludbrook 1963a) may possibly be a dasyurid ancestor of Thylacinidae and, if this should prove to be correct, family rank will probably be sufficient (but see p. 108).

### Thylacinidae Bonaparte, 1838

Only one genus of Thylacinidae is known and the earliest specimen yet discovered came from the upper Pliocene Chinchilla Sand of the Darling Downs of Queensland. Today it is confined to Tasmania where the only living species (*T. cynocephalus*) is rare and possibly verges on extinction.

During the Pleistocene *Thylacinus* was widespread, occurring in Tasmania, continental Australia (where its remains are known from the fluviatile *Diprotodon* Beds of the Darling Downs, various cave deposits in Victoria, New South Wales, South Australia and in south-western Australia as far north as the Namban River), and even in New Guinea where a single mandible was found recently by Dr and Mrs R. Bulmer among pebble tools and flakes in an archaeological excavation near Kiowa in the Eastern Highlands (Van Deusen 1964).

Size, or proportional difference, has been the main criterion used by authors to differentiate the various described species of *Thylacinus*. Thus, *T. breviceps* (which is almost certainly a female and undoubtedly a juvenile specimen: Aust. Mus Sydney No. 774) was described by Krefft (1871) as a small species of modern Thylacine; and *T. spelaeus*[*] of the Pleistocene was described by Owen (1845) as a larger species than *T. cynocephalus*, and *T. rostralis* likewise by De Vis (1894). De Vis claimed for his species that its proportions differed so much from those

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[*] The status of the name *T. major* Owen 1877 is uncertain. The species was figured (Foss. Mamm. Aust. Pl. V.) from the hinder part of a left mandibular ramus with $M_{2, 3, 4}$. $M_3$ and $M_4$ are drawn as having very reduced talonids and are quite unlike those of *Thylacinus* while $M_2$ is an ordinary *Thylacinus* tooth. Lydekker (1887, p. 264) says that *T. major* was apparently given inadvertently for *T. spelaeus* and that the specimen illustrated by Owen was apparently drawn from the last three true molars of *Sarcophilus laniarius* added to the hinder part of a mandible of *T. cynocephalus*. I found no specimen of *Thylacinus* corresponding with Owen's figure in the collection of the British Museum (Nat. Hist.).

## TABLE 1.

*Thylacinus:* Comparison of adult modern Tasmanian population with Western and Eastern (including specimens from New South Wales, Victoria and South Australia east of the Nullarbor) Cave-fossils

| x | | Block 1 | | | | | Block 2 | | | | | Block 3 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Character | | Modern *Thylacinus cynocephalus* | | | | | Western cave-fossil *Thylacinus* | | | | | Eastern cave-fossil *Thylacinus* ( *spelaeus*) | | | | |
| Ref. No. | Morphological Name | x mm | Observed range mm | n | s. mm | V | x mm | Observed range mm | n | s mm | V | x mm | Observed range mm | n | s mm | V |
| 1 | $M^2$ pr.-me. .... | 15·3 | 13·6 16·6 | 52 | 0·9 | 5·76 | 13·0 | 11·4–16·0 | 12 | 1·1 | 8·38 | 15·6 | 14·3 17·1 | 4 | 1·8 | 11·28 |
| 2 | $M^3$ pr.-me. ... | 17·8 | 16·0 19·7 | 46 | 1·2 | 6·50 | 15·4 | 13·2 17·6 | 9 | 1·1 | 7·41 | 17·6 | 15·8–20·2 | 3 | 2·3 | 13·20 |
| 3 | $M^{1-4}$ length.... | 45·5 | 41·7 50·1 | 39 | 2·8 | 6·17 | 40·0 | 36·8–45·9 | 7 | 3·1 | 7·78 | 44·9 | 41·4 50·6 | 3 | 5·0 | 11·16 |
| 4 | $P_4$ length ... | 10·8 | 9·2 11·9 | 56 | 0·6 | 5·27 | 10·7 | 9·3–12·1 | 8 | 1·1 | 9·79 | 11·2 | 10·1 12·3 | 4 | 1·1 | 9·81 |
| 5 | $P_4$–C length ... | 49·4 | 41·1–59·4 | 47 | 4·3 | 8·76 | 49·9 | 38·0 57·9 | 4 | 9·1 | 18·20 | 52·6 | 50·9 54·3 | 2 | 2·4 | 4·58 |
| 6 | $M_4$ length .. | 15·7 | 13·9–17·1 | 46 | 1·0 | 6·20 | 14·9 | 12·8 16·9 | 8 | 1·4 | 9·46 | 16·5 | 14·4 18·6 | 4 | 2·0 | 12·42 |
| 7 | Mand. Length | 175 | 142–206 | 47 | 16 | 9·30 | 163 | 124 189 | 5 | 25 | 15·17 | 159 | 153–165 | 2 | 9·0 | 5·37 |
| 8 | Ht. at $P_4$ ... | 30·8 | 25·8–37·4 | 49 | 2·8 | 9·12 | 29·9 | 24·4–34·8 | 7 | 3·2 | 10·64 | 29·7 | 26·6–33·7 | 3 | 3·7 | 12·3 |

| x | | F | | t. Test | | | |
|---|---|---|---|---|---|---|---|
| Character | | Variance Ratio | | Comparison of Means | | | |
| | | | | Between blocks 1 and 2 above | | Between blocks 1 and 3 above | |
| Ref. No. | Morphological Name | Between blocks 1 and 2 above | Between blocks 1 and 3 above | t | P | t | P |
| 1 | $M^2$ pr.-me. | 1·79 | 4·73** | 8·1119 | <0·01 | 0·6467 | >0·5 |
| 2 | $M^3$ pr.-me. | 1·03 | 3·91* | 5·94 | <0·01 | 0·273 | >0·5 |
| 3 | $M^{1-4}$ length | 1·23 | 3·18* | 4·69 | <0·01 | 0·338 | >0·5 |
| 4 | $P_4$ length ... | 3·41** | 3·70** | 0·2471 | >0·5 | 1·272 | 0·5 0·1 |
| 5 | $P_4$–C length ... | 4·41** | 3·23 | 0·1866 | >0·5 | 0·9029 | 0·5 0·1 |
| 6 | $M_4$ length .... | 2·12 | 4·38** | 1·9636 | 0·1 0·05 | 1·429 | 0·5–0·1 |
| 7 | Mand. length .... | 2·32 | 3·62 | 1·455 | 0·5 0·1 | 1·356 | 0·5–0·1 |
| 8 | Ht. at $P_4$ .... | 1·28 | 1·69 | 0·7802 | 0·5–0·1 | 0·6482 | >0·5 |

* Significant at 5% level. ** Significant at 1% level.

## TABLE 2.

*Thylacinus:* Sexual dimorphism in modern adult Tasmanian population

|  | x | Block 1 |  |  |  |  | Block 2 |  |  |  |  | F | t Test |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Character | modern *Thylacinus* ♀ |  |  |  |  | modern *Thylacinus* ♂ |  |  |  |  |  |  |  |
| Ref No. | Morphological Name | $\bar{x}$ mm | Observed Range mm | n | s mm | V | x mm | Observed Range mm | n | s mm | V |  | t | P |
| 1 | $M^2$ pr.-me. | 14·4 | 13·6–15·3 | 12 | 0·5 | 3·80 | 16·0 | 15·6–16·6 | 10 | 0·3 | 1·85 | 3·409* | 8·092 | <0·01 |
| 2 | $M^3$ pr.-me. | 16·6 | 16·1–17·7 | 11 | 0·5 | 3·18 | 19·0 | 18·3–19·7 | 9 | 0·6 | 2·95 | 1·116 | 9·542 | <0·01 |
| 3 | $M^{1-4}$ length | 42·6 | 41·7–44·1 | 9 | 0·8 | 1·82 | 48·1 | 46·3–50·1 | 9 | 1·3 | 2·71 | 0·283 | 10·878 | <0·01 |
| 4 | $P_1$ length | 10·2 | 9·2–10·7 | 13 | 0·5 | 4·48 | 11·2 | 10·9–11·7 | 10 | 0·3 | 2·63 | 3·349* | 6·467 | <0·01 |
| 5 | $P_1$–C | 46·5 | 41·5–50·9 | 11 | 2·6 | 5·53 | 53·6 | 51·7–55·0 | 8 | 1·3 | 2·5 | 3·674* | 5·151 | <0·01 |
| 6 | $M_1$ length | 14·8 | 13·9–16·2 | 9 | 0·7 | 4·59 | 16·4 | 15·1–17·0 | 9 | 0·6 | 3·67 | 1·276 | 7·825 | <0·01 |
| 7 | Mand. length | 16·1 | 154–173 | 10 | 6 | 3·81 | 189 | 175–198 | 9 | 8 | 1·33 | 1·778 | 8·467 | <0·01 |
| 8 | Ht. at $P_1$ | 28·7 | 26·7–29·9 | 11 | 1·0 | 3·45 | 33·2 | 31·1–36·0 | 9 | 1·6 | 4·77 | 2·561 | 7·107 | <0·01 |

* Significant at 5% level.

of *T. cynocephalus* that it probably also differed from *T. spelaeus* since Owen merely regarded this as a larger Thylacine than *T. cynocephalus*. De Vis said that both *T. rostralis* and *T. cynocephalus* occurred in the Chinchilla Sand.

The phenomenon of "gigantism" is as marked among the Australian Pleistocene forms as it is in other continental faunas and it has generally been believed that *Thylacinus* of the Pleistocene is an example of it. However, records of the presence of *T. cynocephalus* throughout these deposits is a complicating factor; furthermore, in recent years, collections of thylacines from the caves of south-western Australia have been made by the Speleological Group of the Western Australian Naturalists' Club (and in particular by D. L. Cook and R. Howlett, see Cook 1963, 1963a) and these have resulted in the discovery of further material of a very small thylacine of which fragments were first collected in the Mammoth Cave of Western Australia by L. Glauert in about 1909.

It is possible that these reputedly large and small thylacines are merely large and small individuals of a single species and in order to examine this I have, over a considerable period, collected data on thylacines from the British Museum (Nat. Hist.), the Oxford University Museum, the Australian Museum, the National Museum of Victoria, the South Australian Museum, the Queensland Museum, the Queen Victoria Museum Launceston, and the Western Australian Museum. In all, some sixty modern specimens which were collected in Tasmania have been measured in an attempt to gain an indication of the range of variation which might be expected in a fossil population of this genus. It is not possible to give more than a preliminary account of this study here, a study which is complicated by the fact that many specimens are mutilated (particularly the fossils) so that all characters measured are present in only a few individuals and, in the case of the fossils, very few even possess comparable characters. So far the work has been confined to the analysis of single characters but it is hoped ultimately to subject the data to multivariate methods. Here, in order to illustrate the conclusions to date, a selected group of eight separate characters is discussed (*see* Tables 1 and 2).

In *Thylacinus cynocephalus* variances are high. Coefficients of Variation (V) range from about 5-10 but there can be no doubt that only one species is involved in this single living Tasmanian population. The effects of growth have been eliminated as far as possible by selecting characters 1, 2, 3, 4, and 6 because these are dental characters taken on the enamel caps of permanent teeth. In the case of characters 5, 7, and 8 these are certainly likely to be effected by growth since they all include bone, but even these only include measurements from individuals in which dental development is complete.

Excluding the material from the deposits of the Darling Downs, and also the New Guinea specimen, it seems reasonable to divide the remaining fossil specimens into two samples. One of these (Block 3, Table 1), that from the caves of New South Wales, Victoria and eastern South Australia includes the type specimens of *T. spelaeus* from the Wellington Caves, N.S.W. (Brit. Mus. (N.H.) Geol. Nos. M/10800 and M/10801; Fig. 5) while the other (Block 2) is from the caves of the south-west.

The problem of analysis of these samples is complicated by the fact that *Thylacinus cynocephalus* is strongly sexually dimorphic (Fig. 6a and Table 2) and the data have had to be examined to see whether the samples depart sufficiently from normality to render the use of statistical tests invalid when these are constructed on the assumption that they are drawn from populations with normal distributions. It is found that only in the case of mandibular length would there be any doubt about the validity of applying normal statistical procedures.

Tests of variance ratio between modern and fossil samples (Table 1) show significantly different variances. Since the modern population is undoubtedly of a single species, it is tempting to conclude that more than one taxon is included in each fossil sample and that this is responsible for the high variance. However, in the situation where strong sexual dimorphism occurs (and in particular where the sex ratio can be assumed to be 1 : 1, or close to it) the variance cannot be expected to decrease with sample size because both sexes are likely to be represented. Dr. R. D. Hughes, of the Australian

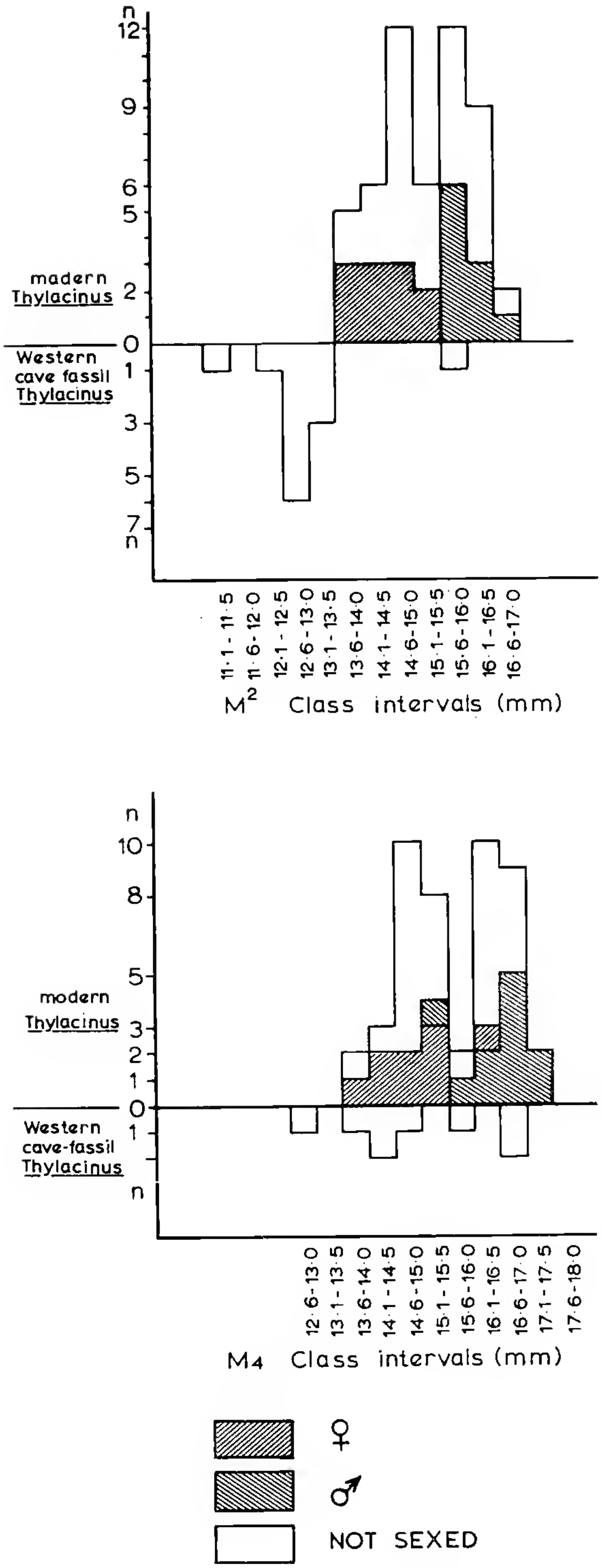

Fig. 6a.—Histograms illustrating the distribution of classes of two characters of modern *Thylacinus* and Western Cave-fossil *Thylacinus*. Where sexes are known these are indicated by different shading.

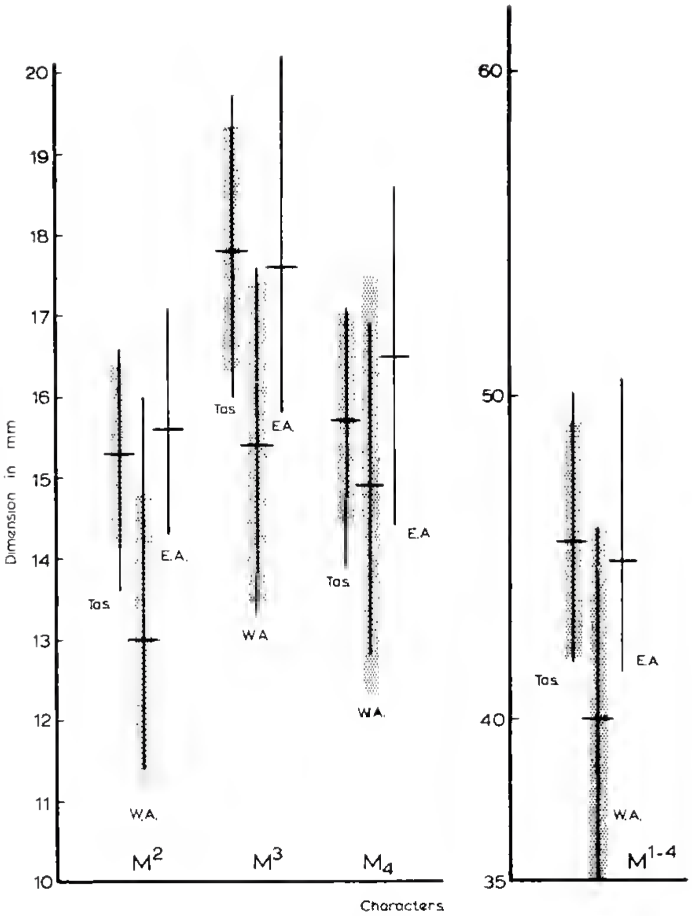

Fig. 6b.—Ranges of values of four characters of three populations of *Thylacinus*. Tas., Tasmanian modern; W.A., Western Cave-fossils; E.A., Eastern Cave-fossils. Vertical lines represent observed range. Horizontal lines represent sample means, stippled blocks superimposed upon Tas. and W.A. samples represent one standard deviation outside the confidence limits of the means. $M^{2}$, $^{3}$ are diagonal measurements across metacone and protocone, $M_4$ and $M^{1-4}$ are measurements of total antero-posterior length.

National University, and I are examining this problem in greater detail and the results will be reported fully elsewhere, but, at present, we are of the opinion that the size of the variances in each of these small samples of fossils are those which might be expected in samples drawn from single species as exemplified by the much larger Tasmanian sample. We conclude that there is no longer any need to postulate sympatry between *T. cynocephalus* and *T. spelaeus* in the Pleistocene of eastern Australia.

Since individuals of *T. spelaeus* are supposed to be larger than those of *T. cynocephalus* their means should differ. Comparison of means by Student's t test (Blocks 1 and 3) shows no significant differences and it can only be concluded that, so far, this work docs not support the separation of these two species.

Comparison between the means of *T. cynocephalus* and Western Cave thylacines reveals a different situation. Here t tests (between Blocks 1 and 2) are significant in characters 1, 2, 3 at the 1% level and approaches significance at the 5% level in character 6. All that now remains is to decide whether the difference is sufficient to warrant the use of a specific or subspecific name. Various approaches to this kind of problem are possible (see Appendix) and it is sufficient to say that using a test which is compounded of the statistical discussions of the 75% Rule of Amadon and the 90% Rule of Mayr, Linsley and Usinger, the characters examined do not support separation even at a subspecific level at the present time (*see* Fig. 6b for a graphic representation of this). However, although recognition by name is not justified there is no doubt that in the Pleistocene of Western Australia there existed a population of *Thylacinus cynocephalus* which on an average contained smaller individuals than the modern form (and by inference its eastern Pleistocene representative).

The status of *T. rostralis* and the thylacines from the two Darling Downs faunas remains unsolved. The Holotype of *T. rostralis* (Queensland Museum F.730, Fig. 5) from Ellangowan nr. Cambooya in south-eastern Queensland is from the Pleistocene fluviatile deposits and lies at the upper end of the range of variation of *T. cynocephalus* (Character 1 of my Table 1 = 15.5, 2 = 17.9, 3 = 47.4, 4 = 12.0, 5 = 58.5, 6 = 17.1, 7 = 203, 8 = 38.9) and the only other specimens from the same beds (Queensland Museum F.3742 from King's Creek, Clifton, 4 = 14.1, 5 = 67.5, 8 = approximately 43; Brit. Mus. (N.H.) 35973 from Gowrie Creek, 1 = 17.1, 2 = 20.2) also have values that are very high. It is thus possible that *T. rostralis* is a distinct form. A value of 18.6 for a single isolated last lower molar (character 6) from the Pliocene Chinchilla Sand also suggests that this form may possibly be distinct as well.

The New Guinea thylacine falls outside the known range of measurements of modern thylacines in at least one character (length of $P_3$). Hobart Van Deusen has a full description of the specimen in preparation for the Novitates series of The American Museum of Natural History. It is hoped that a $C^{14}$ date will also be available.

*Origins.*—The origin of the Thylacinidae is not yet known although Stirton *et al* (1961, p. 35) have suggested that a dasyurid fossil (comparable in size with *Dasyurus viverrinus*) found in Lake Napakaldi in Central Australia may possibly be ancestral because it possess three premolars, graded from front to rear, and lacks a metaconid on $M_1$. But other Dasyuridae (see below) possess a very reduced metaconid on $M_1$ and others have three premolars graded from front to rear and it seems far more likely that a more significant feature of the thylacinid lower dentition, and the one in which it differs from that of advanced Dasyuridae like *Sarcophilus*, lies in the development in thylacine lower molars of a main posterior shearing crest along the ridge from protoconid to hypoconid; this bypasses the metaconid. In the dasyurid line

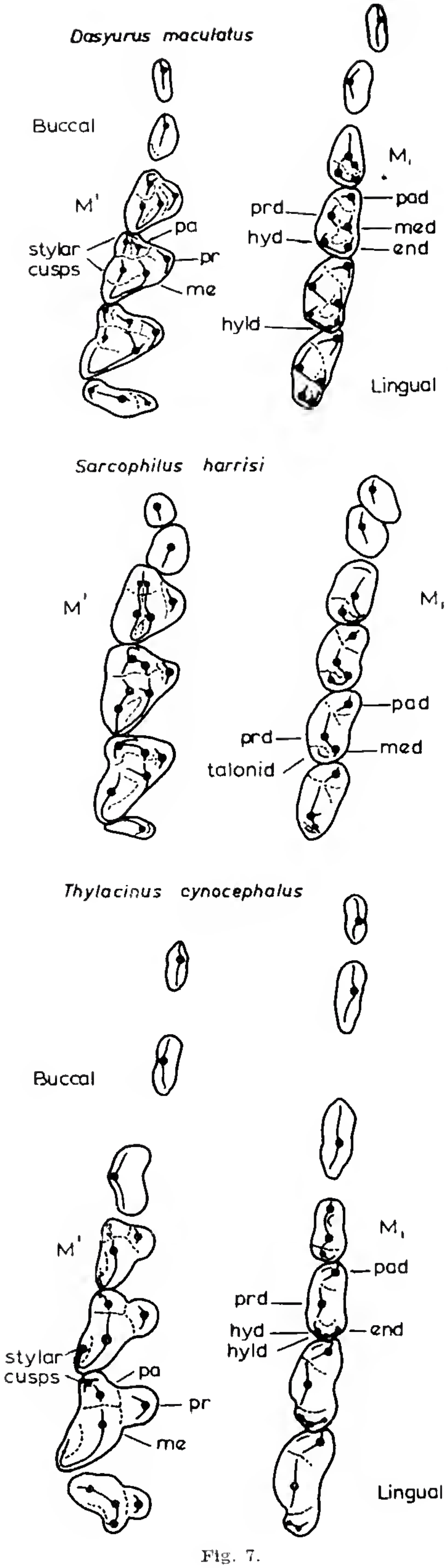

Fig. 7.—Cusps of the upper and lower maxillary teeth of Dasyuroidea. Right upper tooth rows and left lower rows illustrated. Note main differences between *Thylacinus* and others are (a) uppers: *Thylacinus* has poorly developed stylar cusps; (b) lowers: *Thylacinus* has main shearing crest to hypoconid from protoconid; *Dasyurus* and *Sarcophilus* have this to metaconid (pa paracone, pr protocone, me metacone, prd protoconid, pad paraconid, med metaconid, end entoconid, hyd hypoconid, hyld hypoconulid). Ridges are shown in continuous line, valleys in broken line.

Fig. 7.

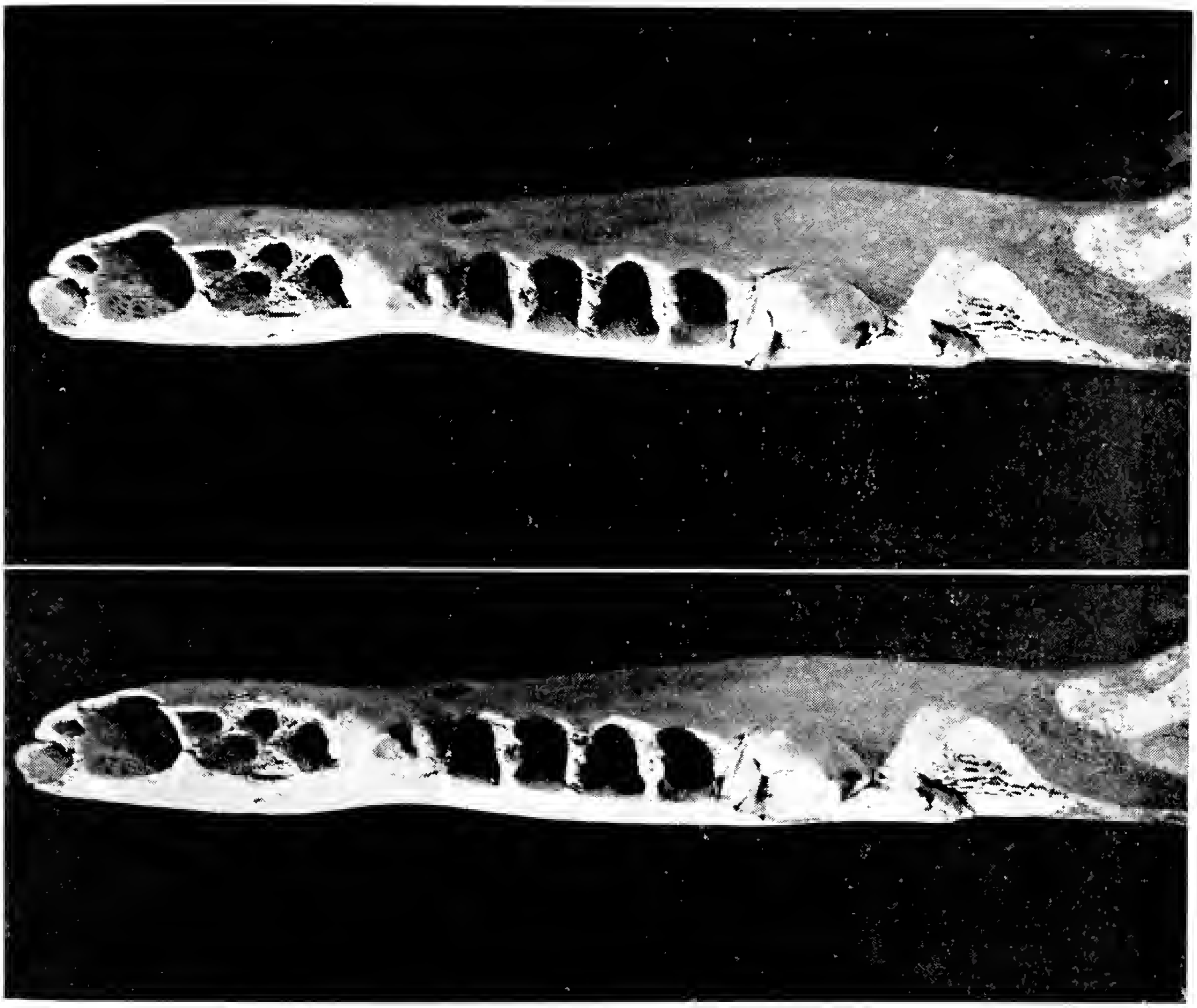

Fig. 8.—Holotype of *Glauccdon ballaratensis* Nat. Mus. Vict. No. P16136 Magnification X2. (Stereo-pair by courtesy Nat. Mus.)

the shearing ridge which is developed is that which runs from the apex of the protoconid; through the tip of the metaconid to the entoconid; in its fully developed form the metaconid is absorbed without trace into this ridge. In both kinds of specialization the metaconid is reduced as its end product, but in the thylacinid line the shear is developed by accentuating the talonid and the hypoconid crest, in the dasyurid line it is developed by specializing the metaconid crest and reducing the talonid (see fig. 7).

Dasyuridae with three premolars which increase in size from front to rear include *Sminthopsis rufigenis*, *S. ferruginifrons*, and *Murexia maxima* (Tate 1947, p. 151, table 5). The metaconid of $M_1$ is so reduced as almost to be absent in the newly described *Antechinus rosamondae* Ride, 1964a (specimen W.A.M. No. M 3421).

## Dasyuridae Goldfuss, 1820

### Dasyurinae

The subfamily Dasyurinae includes a wide range of native cats and their allies including the so-called marsupial mice. It excludes the Myrmecobiinae (the marsupial Banded-anteater). From morphologically greatest to the least, species range from the massive Tasmanian Devil, *Sarcophilus*, through the more typical *Dasyurus*[*], the arboreal treeshrew-like *Phascogale*, their terrestrial relatives *Dasycercus*, the smaller *Antechinus* and *Sminthopsis*, to the minute *Planigale*.

Few fossil dasyurines are known. The oldest is probably the as yet undescribed form mentioned by Stirton *et al* (1961, p. 35) from the

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[*] I follow Simpson 1945 in rejecting Pocock's (1926) concept of four generic names for five species of very similar spotted native cats. These additional "genera" *Dasyurops*, *Dasyurinus*, *Satanellus*, are based in the main upon slight variations in the development of the great toe and in the nature of the footpads. If similar reasoning was to be applied to the related genus *Sminthopsis* (which mercifully has so far evaded the attentions of the splitter) we could have in Western Australia alone up to six "genera" of these. Pocock is also well known as a splitter of eutherian cats (*see* Simpson 1945, pp. 231, 2 for remarks on this and a rather diverting comment on the philosophy of splitting as applied to cats) but it is not generally realized that the present situation in marsupial "cats" is also due to Pocock's attentions.

Etadunna (?Mioc.) formation. This unnamed species has been discussed above under Thylacinidae.

The most important fossil dasyurid yet described is *Glaucodon ballaratensis* Stirton, 1957; its age is not known but is possibly Pliocene (see below). Several Pleistocene species of modern genera have been described. These give little information of phylogenetic importance except perhaps of gigantism.

### *Glaucodon ballaratensis* Stirton, 1957

*Glaucodon* is known from a single almost complete right mandibular ramus which lacks all teeth but the first and fourth molar (fig. 8). It was found in a well at a depth of fifty feet near Ballarat and reached the National Museum of Victoria in 1914. Gill (1957, p. 191), in describing the site, commented that an intensive study is needed before the fossil can be dated with accuracy but the materials in which the well was sunk appear to have been laid down subsequent to the eruptions of the volcanoes which are represented today by Mount Moorookyle and McRorie's Hill. He considers that the deposit is either Pleistocene or Pliocene.

Irrespective of its as yet undertermined age, the fossil is of great interest because it is morphologically intermediate in its few characters between the "normal" large Dasyuridae (e.g., *Dasyurus maculatus*) and the more specialized short-faced Tasmanian Devil *Sarcophilus*. In the skull, these two sorts of Dasyurinae differ principally in the characters associated with the greatly shortened face of *Sarcophilus* coupled with its more extreme development of "carnassial" dentition of the pseudocreodan type (*see* Butler 1946); in *Sarcophilus* great emphasis has been placed on the paraconid crest (particularly between paraconid and protoconid) and the talonid and metaconid are reduced as compared with the ancestral didelphid or even dasyurid molar type (fig. 7). Shortening of the face is a trend which is often repeated among Dasyurinae and it commonly finds expression in reduction and crowding of premolars: examples of it are *Antechinus rosamondae* which may be compared with *A. flavipes*, and *Dasycercus cristicauda* which may be compared with *Phascogale*. Even *Dasyurus* has lost one of the original number of three premolars so that, even in this long-faced genus, shortening has occurred to some extent.

The molar teeth of *Glaucodon* are shown in stereoscopic pair in fig. 8.

In $M_1$, the protoconid is large, there is no paraconid, the metaconid is a small but distinct cone adpressed to the protoconid. The talonid is about one-third of the total length of the tooth. The hypoconid is well developed, the entoconid is small, and there is possibly a small hypoconulid between them. Since the metaconid of $M_1$ is barely present in *Sarcophilus* and it is often almost completely reduced in *D. maculatus*, this tooth may be somewhat more primitive in this respect than either; however the metaconid is closely adpressed to the protoconid and the tooth is particularly reminiscent of that of *Sarcophilus* in its massiveness and lack of lateral compression.

In $M_4$ the protoconid is large and tall and the paraconid is also well developed. The metaconid is somewhat smaller. The main shearing crest of the tooth comprises the ridges from the apices of the paraconid and protoconid, and that between the protoconid and the metaconid (which is set lower than the paraconid). The talonid is much reduced and consists of little more than a hypoconid. The disparity between the heights of the paraconid and metaconid (compare 3 and 4 of Table 3) is a *Sarcophilus*-like character not seen in *D. maculatus* where these two lingual cusps are more or less equal. Although, as mentioned below, the talonid of the $M_4$ of *D. maculatus* may be reduced as much as in *Glaucodon*, in *D. maculatus* the hypoconid and entoconid are separate and even a hypoconulid may be present. In *Sarcophilus* the talonid is usually represented by little more than an isolated cuspule (possibly the hypoconid) posterobuccal to the metaconid, a condition morphologically more like that of *Glaucodon* although advanced on it.

There are few characters in *Glaucodon* upon which to base detailed comparison. However, these are compared with *Sarcophilus and Dasyurus maculatus* in Table 3 (and in figs. 7 and 8). In these few characters the more highly specialized *Sarcophilus* differs from the less specialized *D. maculatus* in having:

(a) An enlarged molar trigonid in comparison with its talonid: in particular it has almost totally reduced the talonid in $M_1$ (2 of Table 3). The trigonid of $M_4$ is also compresed bucco-lingually.

(b) A paraconid which is increased in height relative to the protoconid (3 of Table 3).

**TABLE 3.**

Comparison of characters of *Dasyurus maculatus*, *Glaucodon* and *Sarcophilus*.

| | *D. maculatus* | | *Glaucodon* | *Sarcophilus* | |
|---|---|---|---|---|---|
| | n. | range % | % | range % | n. |
| 1. Total length of $M_1$ as % of length of mandible from anterior tip of posterior edge of masseteric shelf ... | 3 | 29·8–33·2 | 30·6 | 37·8–42·7 | 7 |
| 2. Length of $M_1$ excluding talonid as % of total length of $M_1$ ... | 5 | 67·7–77·1 | 77·0 | 92·0–97·4 | 8 |
| 3. $M_1$ height of paraconid as % of protoconid | 5 | 52·6–63·3 | 56·1 | 63·4–72·2 | 6 |
| 4. $M_4$ height of metaconid as % of protoconid ... | 5 | 52·6–60·7 | 42·7 | 31·3–38·0 | 6 |
| 5. Depth of mandible expressed as % of length of mandible from anterior tip to posterior edge of masseteric shelf | 4 | 15·7–16·7 | 20·5 | 21·7–23·0 | 7 |
| 6. Depth of mandible expressed as % of molar tooth row | 3 | 49·8–56·2 | 51·9 | 51·5–58·9 | 7 |

(c) A metaconid which is reduced in height. This is almost a vestige in some molars (4 of Table 3).

(d) Incisor alveoli which are much crowded so that the alveolus of the second incisor is raised above the plane of the other two (this condition occurs in *D. maculatus* but it is not as well marked).

(e) Premolar alveoli which are crowded, each pair being set at an angle to the long axis of the ramus. There are no diastemata between them.

(f) The depth of the mandible is proportionally greater in comparison with its length (5 of Table 3).

(g) The molar tooth row is proportionally longer in comparison with the length of the mandible (1 of Table 3).

*Glaucodon* compares with these in the following way:

(a) The trigonid of $M_1$ is compressed buccolingually and the talonid is more reduced than in most *D. maculatus* (although I have measured a specimen of *D. maculatus* which had a talonid which was reduced to a similar degree —see Table 3).

(b) The height of the paraconid of $M_1$ as compared with that of the protoconid is within the range of *D. maculatus* and not of *Sarcophilus*.

(c) The metaconid is greatly reduced towards the condition in *Sarcophilus*.

(d) The incisor alveoli are as in *Sarcophilus*.

(e) The premolar alveoli are as in *Sarcophilus*.

(f) The depth of the mandible, expressed as a percentage of its length, is intermediate between that of *D. maculatus* and *Sarcophilus*.

(g) The length of the molar tooth row, as a percentage of the length of the mandible, is within the range of *Sarcophilus* and not of *D. maculatus*.

In all, as far as its known characters go, there is little doubt that *Glaucodon* can be regarded as structurally ancestral to *Sarcophilus*. In some characters it still lingers on the *Dasyurus* side and in others it is clearly *Sarcophilus*-like. In one character (the well developed conical but adpressed metaconid on $M_1$) it is like neither.

### *Dasyurus affinis* and *D. bowlingi*

*D. affinis* McCoy (?1862) and *D. bowlingi* Spencer & Kershaw (1910) are the only two species of fossil *Dasyurus* which have been described to date.

The name *D. affinis* was published in Quarter Sheet N.W. of the Geological Survey of Victoria in a note which merely states "*Dasyurus affinis* (McCoy) New Species nearly as large as *D. maculatus* but differing in proportions". The material comprises two syntypical left mandibular rami (Nat. Mus. Vict. P 7426, P 15101) which have since been figured by Gill (1953b). Gill advises me that the precise locality of the cave from which the specimens come is in basaltic tuff, under a flow of Newer Basalt on a small tributary near the head of Toolern Creek, 4¾ miles S. of Gisborne and 1½ miles S.W. of Couangalt Post Office. The material is Holocene and no revision of the status of the species has been published to date.

*D. bowlingi* is from the dune sands of King Island and Deal Island in Bass Strait and the measurements and other data presented by Spencer & Kershaw of a good series of specimens suggest that the species was much larger and also morphologically distinct from *D. maculatus* with which it was sympatric. The geological age of the material is not known but Spencer & Kershaw infer that the species persisted into modern times and was seen alive by Péron during the Baudin expedition of 1801.

### *Scarcophilus laniarius* and *S. prior*

*S. laniarius* (Owen, 1838) and *S. prior* De Vis (1883) are the only two species of fossil *Sarcophilus* which have been described to date although Stirton (1957, p. 131) records an undescribed species from the Pliocene at Kalamurina, on the Warburton River, South Australia, which he says is closer to *S. laniarius* than to *S. harrisi* Boitard (the modern species).

It is widely accepted that *S. laniarius* is a gigantic Pleistocene form of the modern species and Gill's (1953, p. 87) statement of mandibular measurements "from 15 to 50 per cent. larger than the average extant *Sarcophilus*" suggests that, unlike the position in *Thylacinus spelaeus* and *cynocephalus*, the distinction between the two should be maintained.

*Sarcophilus prior* De Vis, 1883 comprises only the proximal articular surface of a right tibia with a little of the shaft. It is from "Darling Downs" and is somewhat larger than the corresponding bone in the modern specimen of *Sarcophilus* with which De Vis compared it.

### Myrmecobiinae

There are no fossils and nothing significant has been added to the problems of the affinities of *Myrmecobius* since the beginning of the century. During the 19th century *Myrmecobius* was believed to be an unmodified survivor from the Jurassic with affinities with Mesozoic mammals, but the modern view which can be directly attributed to Bensley is that its unusual dental characters (and among these its high dental formula) have been derived from those of normal Dasyuridae. Bensley (p. 100) said that many of the characters of the incisors, canines, and premolars "which appear at first sight to be primitive, are repeated in the Peramelidae, where they are undoubtedly the result of retrogression. The patterns of the lower molars are directly derivable from those of the smaller Dasyurinae", and of the upper molars Bensley is also of the opinion that the basic pattern which can be recognized running through these very variable teeth is approximately that characteristic of normal Dasyurinae as well. Great dental aberration is characteristic of myrmecophagous mammals (e.g. *Proteles*, the Aard-wolf).

For a while, the phylogenetic picture was somewhat confused by the description of the fossil *Myrmecoboides* (Gidley, 1915) from the

Mid Palaeocene of North America. This now turns out to be a eutherian insectivore and may be disregarded in this context (Simpson 1945, p. 172).

## PERAMELINA

Even less is known of the Peramelina as fossils than the Australian Marsupicarnivora with the exception of enormous numbers of specimens of modern species in the Pleistocene cave deposits of various parts of Australia.

The modern bandicoots appear to fall into at least two distinct groups, one of these includes only the Rabbit Bandicoots (*Macrotis*) while the others are obviously fairly closely related, with the Pig-footed Bandicoot (*Chaeropus*) as a highly specialized derivative. *Perameles tenuirostris* Owen, 1877 and *Perameles wombeyensis* Broom, 1896b have both been described from the Pleistocene of New South Wales.

There has been no revision of the status of *P. wombeyensis* but, from what I know of the fauna from the Wombeyan Caves, N.S.W. which contains it (Ride 1960) I would not be surprised to find that it is identical with a modern form.

*Perameles tenuirostris* (Owen 1877, Pl. V., figs. 10, 11) is from the Wellington Caves, N.S.W. and is stated by Lydekker (1887, p. 255) to be identical with the modern *P. nasuta*.

*Ischnodon australis* Stirton (1955) is the only Tertiary species which has been described.

### *Ischnodon australis* Stirton, 1955

This fossil bandicoot which comprises a single fragmentary mandibular ramus with two premolars and two molars in position was described from the late Tertiary Palankarinna Fauna from the Mampuwordu Sands at the Woodard Quarry near Etadunna Station, South Australia. Stirton was unable to determine the exact relationship of the bandicoot (see Fig. 9) but he suggested that it was nearer to the rabbit bandicoots (*Macrotis*) than to other Peramelidae. In particular, he considered that the presence of a somewhat reduced paraconid and reduced hypoconulid on the molars indicated relationship to *Isoodon* and *Perameles* but the fact that they were reduced although present suggested *Macrotis* relationships where (he implies) the paraconid is lost.

Comparison of Stirton's figure and measurements with *Macrotis* in the collection of the Western Australian Museum reveal that his generic diagnosis includes some specimens of *Macrotis lagotis* because some of the details of dentition which he regarded as being of generic value, i.e. the presence of a much reduced paraconid and hypoconulid, and the presence of a small stylar cusp antero-buccal to the hypoconid, are very variable in that species. In fact all these characters of *Ischnodon* are present in specimens WAM No. M 1399 from Bridgetown in south-western Australia, and WAM No. M 632 from Laverton, W.A., yet, as Stirton has implied, other specimens lack the paraconid completely (e.g. WAM M 898 from Wiluna).

The only feature of *Ischnodon* at present described which I consider to be of significance are its low crowned molars which are lower than those of any rabbit bandicoot known to me. For the present, the generic distinction can only be maintained in this respect.

## DIPROTODONTA

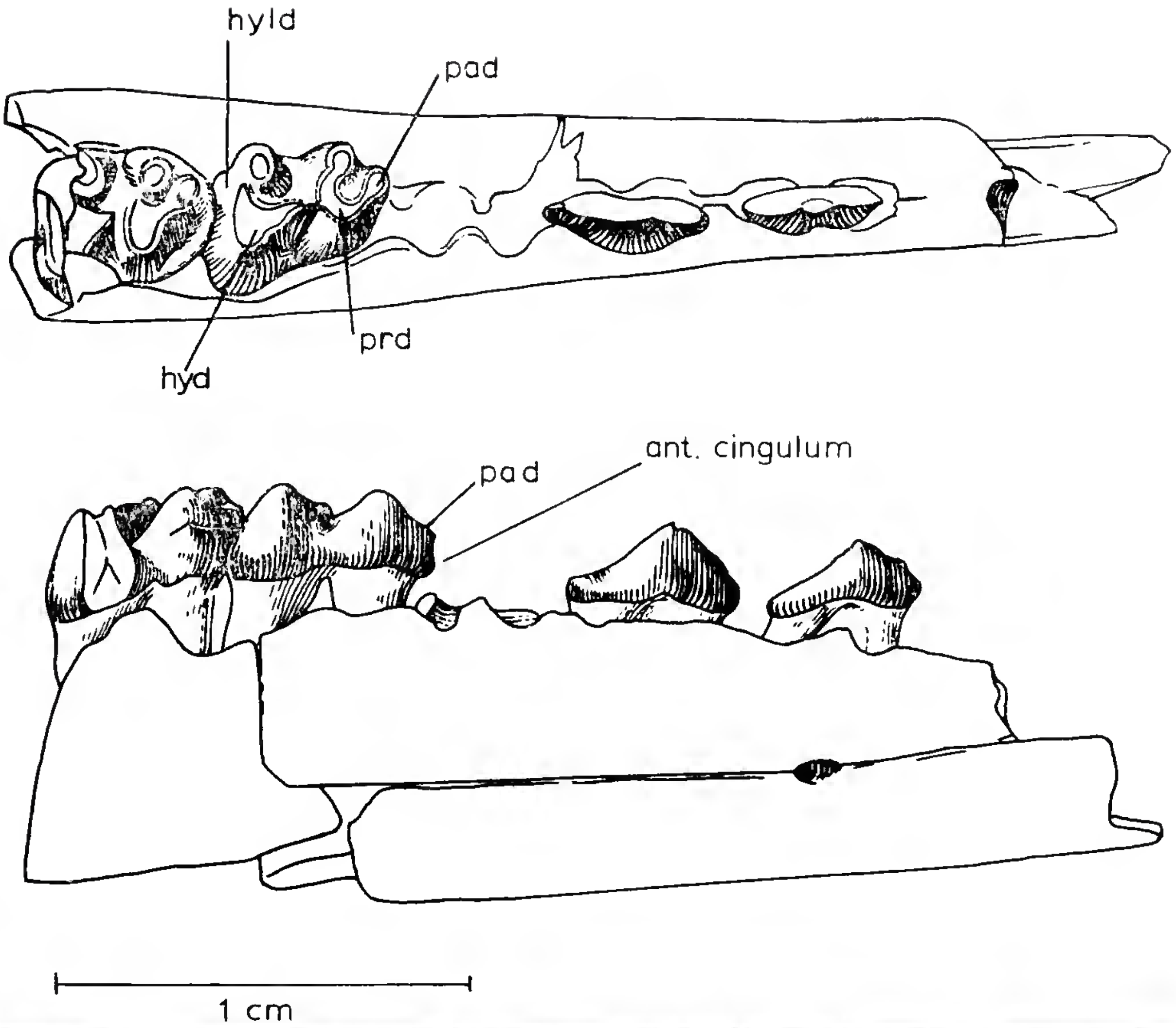
The Diprotodonta is the most diverse, and to me most structurally interesting, of all the marsupial orders. It is generally thought of as a herbivorous order but it actually contains a complex series of radiations within itself. Primitive modern members of it (Bensley 1903, p. 124) are insectivores (e.g. the small modern phalangers such as *Distoechurus* and *Cercartetus*, and in addition it contains at least one rapacious carnivore (*Thylacoleo*), and several smaller modern forms with strong carnivorous tendencies (*Bettongia*). There are many herbivores of browsing and grazing habit and there is even a fossorial bear-like animal (the Wombat). Among the browsers and the grazers were the heavy "pachydermatous" Diprotodontidae, the gazelle and cervid-like Macropodinae, and their close relatives the browsing-adapted bovid-like Sthenurinae (*see* Ride 1959 discussion of *Procoptodon*). Some of these phyla have even become convergent upon each other as have the diprotodontid palorchestines upon kangaroos (Woods 1958, Bartholomai 1962).

The known Pleistocene fossils, of which there are many, are mainly of large and moderately large animals and help us to fill out the details of this great radiation; the great numbers of them and their diversity gives to Diprotodonta a much better appearance of balance of knowledge between fossils and living genera. However these appearances are still misleading because we have no lineages and thus can talk only of evolutionary lines by arranging Recent or Pleistocene animals in order of primitiveness and arguing from them.

The sub-taxa of Diprotodonta which may be distinguished by this means comprise five and possibly six distinct phyletic lines. These are the Phalangeridae as represented by the modern Australian Possums, Cuscuses, Flying Possums, Pigmy Possums, etc. and Pleistocene forms including *Thylacoleo;* the Macropodidae as represented by the modern Kangaroos, Wallabies and Rat Kangaroos (these latter may be widely separate from true Macropodidae and, in modern taxonomic practice it is usual to separate them off as a subfamily Potoroinae); the Diprotodontidae as represented by the giant extinct forms *Nototherium, Diprotodon, Palorchestes,* etc.; the Vombatidae which comprises the Wombats and their extinct giant relatives; and the Wynyardiidae which contains only *Wynyardia bassiana* of

Fig. 9 (opposite).

Fig. 9.—Upper figure: Holotype of *Ischnodon australis* after Stirton 1955. Stereo-pairs of mandibles of *Macrotis lagotis* for comparison of paraconid, hypoconulid and cuspule between protoconid and hypoconid. (Upper pair WAM No. M632, Laverton, W.A. Lower pair WAM No. M1399, Bridgetown, W.A.) Upper pair show $dP_4$ in position. In lower pair $P_4$ is erupting. Stereo-pairs and line drawing not to same scale.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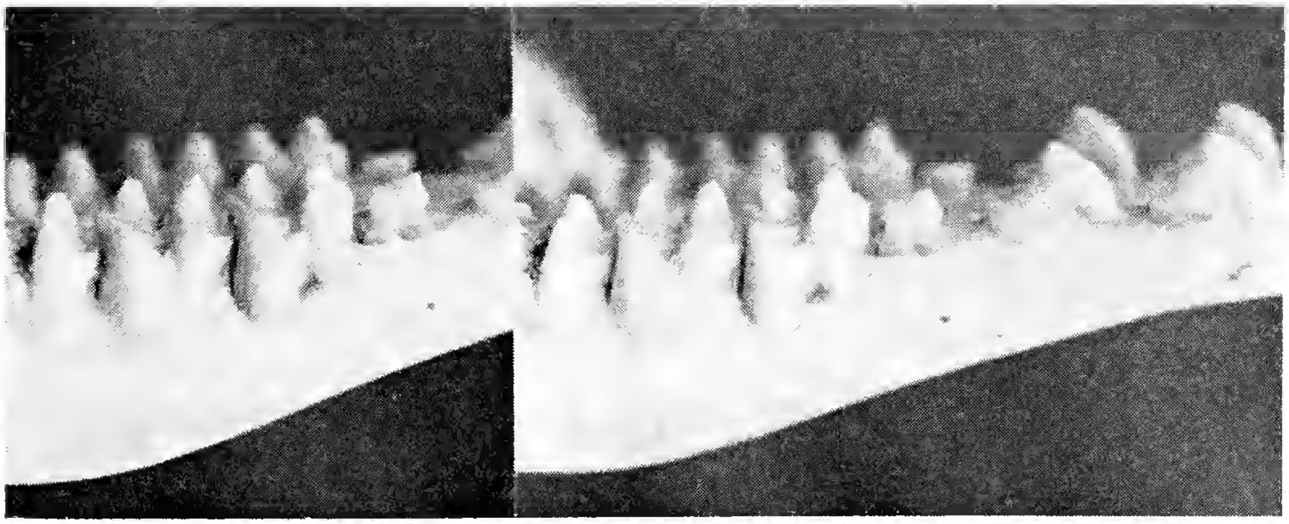

the Oligocene. In addition there is possibly a separate line containing only the Koala *Phascolarctos* (*see* Troughton 1959, pp. 75 and 84 for a discussion of the problems of the relationships of *Phascolarctos*).

### Wynyardiidae Osgood, 1921

### *Wynyardia bassiana*

The oldest diprotodont known to us is *Wynyardia bassiana*, a remarkably complete and semi-articulated skeleton from the Oligocene which was found prior to 1876 at Fossil Bluff near Wynyard in Northern Tasmania. It received numerous mentions in literature (Gill 1957) before being described by Sir Baldwin Spencer in 1900 (Spencer 1901). Unfortunately, Spencer was so impressed by its great age (at that time thought to be basal Eocene) that he made rather extravagant claims for it on the basis of a detailed description and discussion of its characters—a discussion based upon inadequate* material of other marsupials.

Spencer concluded that *Wynyardia* was intermediate between the "Polyprotodonts" (Marsupicarnivora and Peramelina) and Diprotodonts and moreover that it possessed a number of characters unknown in any other marsupial. Subsequently, Wood Jones became interested in this fossil and ultimately obtained the loan of its principal parts for redescription. Unlike Spencer, he concluded that the fossil had no non-marsupial characters, that it had no specifically non-diprotodont characters, and that it must be considered an ally of the phalangers but probably differed from the modern lightly built animals in both gait and bodily habit.

Unfortunately, Wood Jones, always a direct man, demonstrated his disagreement with Baldwin Spencer's conclusions in a manner which has allowed subsequent workers to misinterpret his results and moreover to misread his conclusions. Thus *Wynyardia* has come to be regarded as an animal very much like the modern possum *Trichosurus* (*see* Gill 1957). Admittedly, Wood Jones claimed that *Wynyardia* had many resemblances to *Trichosurus* but this claim was in the main because his results were based almost entirely upon comparison between the fossil and a similarly mutilated specimen of *Trichosurus* (*see* Wood Jones 1931).

Thus a suspicion arose that *Wynyardia* might even have been a modern possum which had fallen into a fissure in the limestone and had become incorporated into the Fossil Bluff sequence (Gill 1957 gives an excellent account of this).

The most important recent work on *Wynyardia* has been done by E. D. Gill, Curator of Fossils at the National Museum of Victoria. By using physical and stratigraphical methods he reexamined the provenance of the fossil and concluded that it was undoubtedly contemporary with the Fossil Bluff fauna and is not a subsequent inclusion. Today, this fauna is considered to be Oligocene‡ (Gill 1962, p. 249).

The establishment that the fossil was genuine together with the misinterpretation of Wood Jones' results has resulted in claims being made that the Possum (i.e. *Trichosurus*) has an antiquity dating back to the Oligocene (*see* Gill, 1955, p 92). Results of examination by myself (the full details of which will be published elsewhere) do not support this view and reveal that, contrary to current opinion (which has grown like a snowball around a slender nucleus of misinterpreted results), *Wynyardia* is a very remarkable animal quite unlike any known diprotodont combining as it does a number of very primitive marsupial characters with robustly expressed specializations peculiar to itself. Any resemblance to *Trichosurus* which the fossil possesses is in those characters which represent relatively unspecialized diprotodonty.

*Wynyardia* comprises a broken skull (fig. 10), the inferior border of the left mandibular ramus, a coronoid process (which has become lost since Spencer's examination), the axis vertebra, a series of nine articulated presacral vertebrae including the last thoracic, portions of fused sacral vertebrae, a large portion of pelvis comprising the dorsal ramus of the right ischium including the acetabulum, and a more or less complete right ileum, one epipubic bone, a more or less complete left femur and a fragmentary right femur, the left tibia and fibula, together with some fragments of ribs. At the time of Baldwin Spencer's and Wood Jones' examinations, the skull, mandibular ramus, long bones of the hind limb, sacrum, and pelvic fragments had been extracted from the matrix. After Wood Jones examined the material, the vertebral column had also been extracted and was available for examination. The otic region was still filled with matrix and glue and I removed these.

That *Wynyardia* is a diprotodont is established by the presence, at the anterior end of the mandible, of the unmistakable root of a single large incisor and as Wood Jones pointed out, the upper incisor alveolus which remains in the premaxilla is consistent with its having an enlarged first upper incisor of phalangerid type. Along the broken dorsal margin of the mandibular ramus there are four circular structures which are almost certainly the broken tips of the roots of cheek teeth, these are followed by a pathological cavity and what is almost certainly the alveolus of the last molar. If this mandible and these "teeth" are then positioned on the skull it will be seen that the anterior end of the zygomatic arch lies midway along the toothrow; this is another diprotodont character not found in Dasyuridae or Peramelidae. In these it lies at the posterior end of the toothrow. The position of the posterior end of the palate is indicated by the pterygoids and confirms this. The pterygoid fossa in the mandible can also only be matched in Diprotodonta among Australian forms.

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* Comparison by Spencer with an inadequate series and insufficient information regarding variation is the only way in which I can interpret the mis-statements of marsupial anatomical detail which he makes. The mis-statements do not relate so much to the fossil (of which his description is excellent) but in regard to the distribution of various characters among living Marsupialia.

‡ Spencer's geological contemporaries regarded it as "basal Eocene" while Wood Jones followed Chapman's "no older than the Miocene" and Howchin's "no older than the Pliocene" (Jones 1931, p. 97).

Primitive characters found in no diprotodont are best seen in the region of the middle ear (*see* stero pairs in fig. 10 a, b). Unfortunately, the bullar wing of the alisphenoid has been broken away and the tympanic is missing but sufficient completely undamaged surface on the post-glenoid process remains to show that the tympanic was not tubular and fused to the post-glenoid process as in Diprotodonta in spite of Wood Jones' statement that the post-glenoid process and the auditory region do not differ from that of *Trichosurus*. He argued that the smooth surface of the post-glenoid process might be due to erosion but this is not so; except for about 3 mm of its postero-mesial end (length 12 mm), the structure is covered by a finished surface which is quite unlike the ragged cancellar appearance of an eroded contact area from which a fused tympanic tube has been torn. On the other hand, I suspect that the innermost 3 mm which is eroded does represent the point of contact with the tympanic ring (the differences between the post-glenoid and tympanic region of *Wynyardia* and *Trichosurus* can be seen in fig. 10 b, d) and if this is so, it could represent an intermediate stage between the free ring of Didelphidae and the fused tube of the Phalangeridae.

The most important primitive character of the middle ear of *Wynyardia* is the complete absence of epitympanic sinuses either anterior or posterior to the epitympanic recess. Van der Klaauw (1931, p. 82) says that these sinuses are absent in monotremes and didelphids, while other marsupials show well-developed sinuses in the squamosal. The very small epitympanic recess between the periotic and the portion which remains of the tympanic wing of the alisphenoid suggests that the alisphenoid bulla was at most very short and merely shielded the epitympanic recess. In fact, in general appearance the whole region is almost identical with that of modern *Didelphis virginiana* (fig 10 c) except that the anterior face of the periotic is slightly more flattened in the fossil which suggests that the tympanic wing might have contacted it here. The morphology of the squamosal behind the ear and its entire relations in the nuchal and post-glenoid regions are also completely unphalangerid and can be matched only in Marsupicarnivora.

Other characters of a marsupicarnivoran aspect, although probably of less importance being inherited by other Diprotodonta, are the shape of the nasals which are precisely those of *Didelphis*, the lachrymo-nasal contact, the great sagittal crest, the very short post-tympanic region, and the position of the sacral articulation in the ilium. This is very far anterior as in *Didelphis*, not mid-way to the acetabulum as in Phalangeridae. The triangular cross section of the ilium is also typically *Didelphis*-like.

Some of the specializations of *Wynyardia* seem to be related to its extremely robust build and, probably, erect carriage of the body which must have been somewhat Koala-like. This robustness is represented in the skull by the depth of the mandible (only the tips of the roots of the cheek teeth are present along the broken dorsal surface so that it seems certain that much is missing of the ramus which is already not much more slender than the mandible of *Trichosurus*) and by the large areas of attachment of the pterygoid and masseter-temporal muscle groups. It is in the post-cranial skeleton however that adaptations to an erect or semi-erect posure are most marked. Lumbar vertebrae, which are typically phalagerid in possessing well developed slender anapophyses (hyposphenes), have transverse processes which are horizontal and form an acute angle with the plane of the anterior zygopophyses. This acute angle is only exceeded by the Koala (and approached by the cuscus). The koala and the cuscus are both animals which habitually adopt an erect position. The pelvic girdle suggests the same conclusion. The epipubes are very large; in modern Diprotodonta they are largest in the Koala (approximately half the length of the femur); in *Wynyardia* even the incomplete epipubis is greater than half the length of the femur (64.7 mm: 106.4 mm). On the ilium, which is triangular in section, the area of origin of the gluteus medius is large (*see* Elftman 1929 for terminology) which agrees with the observation that the greater trochanter of the femur (which carries its insertion) is also large. On the other hand the lesser trochanter is smaller than that of *Trichosurus* or *Phalanger* and this agrees well with the observation that the area of origin of the iliacus on the ilium is smaller in *Wynyardia* than in these genera. The acetabulum is strongly buttressed anteriorly. These features would argue (*see* Elftman 1929, p. 213) that the animal was able to remain for considerable periods in the upright position where the gluteus medius would be one of the muscles concerned in its support.

The bones of the hindlimb are robust and the tibia is short as compared with the femur. The fibula is also much closer to the tibia in size than is that of modern phalangerids (e.g. *Trichosurus*). However, it is of phalangerid form as distinct from that of Macropodidae or Peramelidae (*see* Barnett & Napier 1953, p. 209). In all, it would seem that the specializations of the postcranial skeleton and in particular the robustness of the bones of the hindlimb, the proportions of tibia and fibula, and the shortness of the distal part of the limb in comparison with the femur, suggest that *Wynyardia* was a slow, deliberately moving animal without saltatory or cursorial specializations.

Since *Wynyardia* is so very different from all known phalangerids—an Oligocene diprotodont with clear evidence of marsupicarnivoran origins of a didelphid kind, but yet highly specialized in its own peculiar way—I follow Osgood (1921) in including it in a separate family which will include those primitive diprotodonts which combine diprotodonty with a primitive middle ear which (like that of *Didelphis*) lacks epitympanic sinuses.

### Phalangeridae Thomas, 1888

The Phalangeridae is the stem family of the Diprotodonta with the Wynyardiidae (as defined here) at its base; although the *Wynyardia* itself is probably too specialized to be directly

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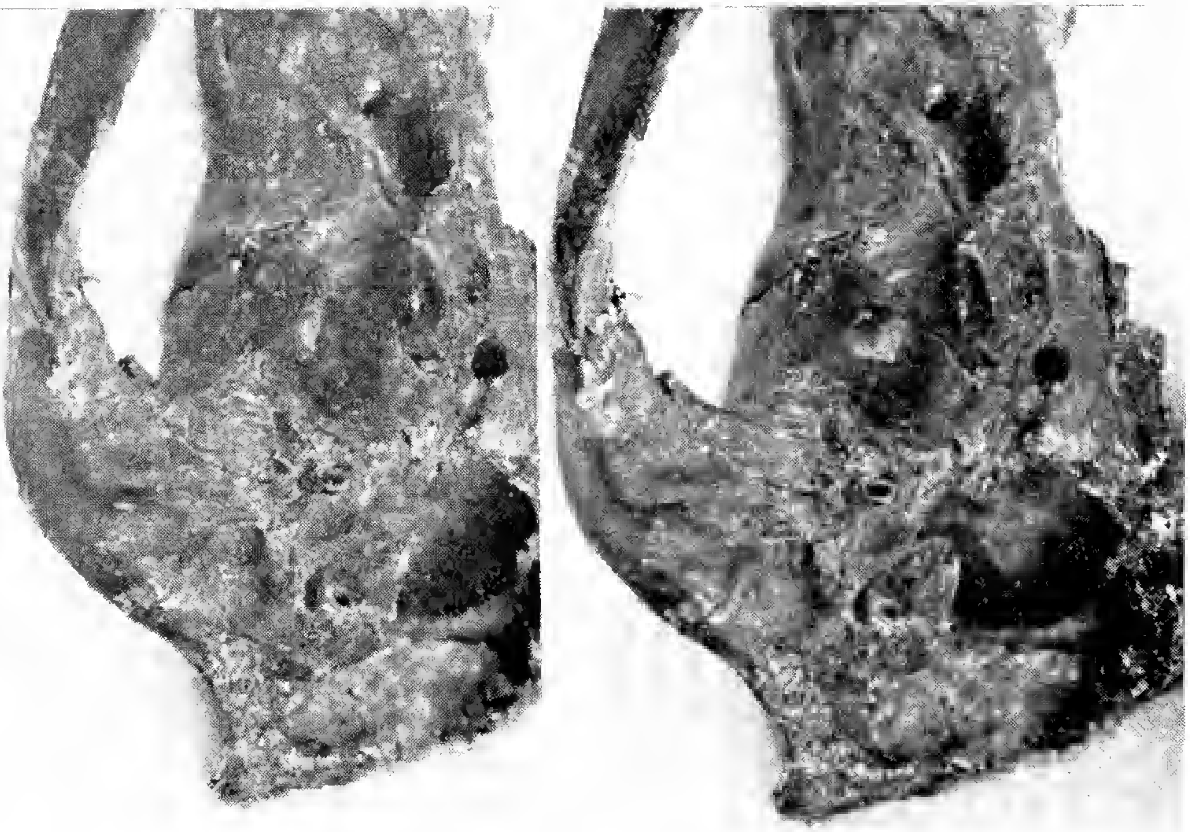
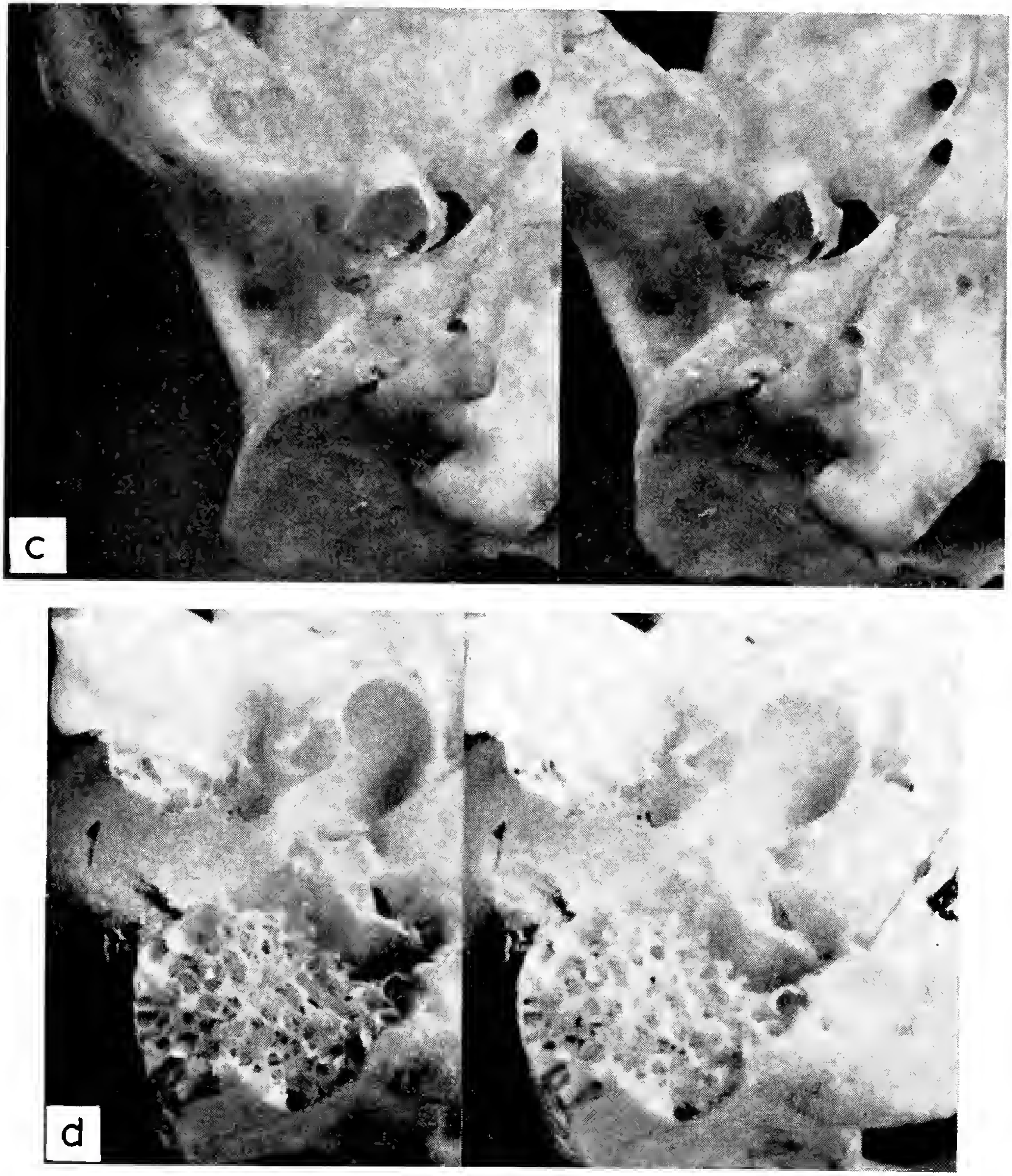


b

Fig. 10.—*Wynyardia bassiana*. (a) Ventral view of skull. (b) Otic region. (c) Otic region of *Didelphis virginiana* for comparison. (d) Otic region of *Trichosurus vulpecula* for comparison. In *Trichosurus* the tubular tympanic meatus has been broken away from the post-glenoid process and from the squamosal. The floor of the alisphenoid bulla has also been removed to reveal the epitympanic sinuses for comparison.



ancestral. Offshoots which are probably pre-Miocene in time of separation are the Vombatidae, the Diprotodontidae, and the Macropodidae.

The main stock is the Phalangerinae, a subfamily which contains all of those forms which Bensley regards as basal in dentition to the phalangerid radiation (including *Acrobates*, *Distoechurus*, *Eudromicia*, *Cercartetus*), as well as certain larger forms which have progressed beyond the insectivorous habit but which, nevertheless, have remained rather generalized in molar form (*i.e. Petaurus*, *Trichosurus*, *Wyulda* and *Phalanger*).

The Tarsipedinae, which is probably a relatively modern offshoot, contains only the highly specialized nectar-feeding *Tarsipes* which thus occupies a position analogous with that of *Myrmecobius* in the Dasyuridae; and, as is the case there, fossils are unknown.

The Phascolarctinae, as it is at present recognized, includes the Koala *Phascolarctos*, the ringtails *Pseudocheirus* and the Greater Glider *Schoinobates*. These are selenodont in dentition but there is very great suspicion that too much phylogenetic emphasis has been placed on this character (*see* below and Troughton 1959, p. 84).

The Thylacoleoninae comprises the marsupial lions. Obviously derived from large phalangers, they represent the supreme diprotodont adaptation to the rapacious habit, a habit which is not strange to some of their smaller relatives. Two species are known. *T. carnifex* Owen is the typical Pleistocene form and *T. crassidentata* Bartholomai (1962) is a slightly less highly evolved form from the Pliocene Chinchilla Sand. Woods (1956) has revised *Thylacoleo*. Gill (1954) discusses habits and distribution and provides a full bibliography.

Most of these forms of Phalangeridae are fairly small animals and accordingly it is not surprising that there are only a few fossils beyond the owl pellet deposits of the Upper Pleistocene and Recent. Of the phalangerid fossils the earliest and most important is *Perikoala palankarinnica* Stirton, 1957a from the Miocene of the Etadunna Formation; a form which Stirton places in the Phascolarctinae.

Of the Pleistocene species of Phalangeridae only one has been sufficiently spectacular to have played an important part in phylogenetic speculation. This is *Burramys parvus* from the Wombeyan Caves of New South Wales. A brief discussion of *Perikoala* and *Burramys* is included here.

### *Perikoala palankarinnica* Stirton, 1957

*Perikoala* was originally described as part of the Palankarinna ?Pliocene fauna but Stirton *et al* (1961, p. 36) now refer it to the underlying Miocene Etadunna Formation.

Unfortunately, this remarkable fossil is only known from very fragmentary material: an edentulous maxillary fragment and a broken mandibular ramus with a broken last lower premolar and the first two molars which are almost complete. I have not seen the material but Stirton (1957a) says that it resembles both *Trichosurus vulpecula* and *Phascolarctos* and he concluded that *Perikoala* was clearly phascolarctine, presumably because of the crenulated enamel in the basins of the teeth and because of the wide separation of hypoconid and entoconid in the posterior premolar which (although only a fragment of it remains) was obviously unusually molarized for a phalangerid. In large Phalangerinae (e.g. *Trichosurus*, *Phalanger*, and *Wyulda*) this tooth is specialized as a sectorial and not broadened as in *Phascolarctos*. As compared with *Pseudocheirus*, *Schoinobates* and *Phascolarctos*, *Perikoala* is not selenodont (or subselenodont) but quadriscuspid or even bilophodont yet it has the large number of small folds in the crenulated enamel so typical of the Koala.

The modern practice of separating the Koala, the Ringtails, and the Greater Glider from the Phalangerinae because of their selenodonty (subselenodonty) follows such authorities on dental morphology as Bensley (1903, p. 135); he and various earlier workers were so impressed by the appearance in some marsupials of selenodont dentition, that they could not avoid drawing parallels between them and the selenodont and bunodont sections of the eutherian ungulates and hence placed great phylogenetic weight on this character. Accordingly, *Phascolarctos* was placed with *Pseudocheirus* and *Schoinobates* in a separate subfamily. The molars of *Perikoala* and *Phascolarctos* are undoubtedly similar in their crenulations but it is timely to remember Thomas' statement (1888, p. 167) in relation to *Pseudocheirus* that "this genus, with its close ally *Petauroides* (*Schoinobates*), by the complicated subselenodont character of its molars, stands somewhat apart from most of the other Phalangers, and approaches *Phascolarctos*, in which a rather simpler form of the same modification is observable. In young Cuscuses, however, a tendency towards the same structure is also visible, but the crests on the molars soon wear off, and then there appears but little difference between their molars and the simple smoothly quadricuspid ones of *Petaurus*, *Dactylopsila*, and their allies."

In fact, one cannot help wondering whether the relationships of *Phascolarctos* and *Perikoala* might not lie with *Phalanger*, rather than with *Pseudocheirus* with which *Phascolarctos* bears scarcely any resemblance except in the questionable selenodonty of its molars. When more is known of *Perikoala*, it may provide a useful indication here.

### *Burramys parvus* Broom, 1896

*Burramys parvus* Broom is a very small phalangerine with very large sectorial premolars (fig. 11) which closely resemble those of *Hypsiprymnodon*, (which is in some respects the most primitive of the Macropodidae, and of *Propleopus* the giant Pleistocene rat-kangaroo. Until recently, *Burramys* was only known from a single deposit, the ?Upper Pleistocene Broom fauna of the Wombeyan Caves, New South Wales (Ride 1960). Wakefield (1960) has since obtained it from Buchan in Victoria.

Because of its remarkable premolar, Broom described *Burramys* as a link between the phalangers and kangaroos, and later (Broom 1898) even concluded that it was "probably very closely allied to the small *Phalanger* from which *Thylacoleo* was descended". Ultimately Tate (1948), without further examination, removed *Burramys* into the Macropodidae from the Phalangeridae.

In 1956 I revised the status of *Burramys* following re-examination of some of Broom's original material and some additional specimens which were prepared from breccia collected by Broom at the type locality. *Burramys* was shown to be a phalangerid whose supposed macropod affinities rested solely upon the structure of the premolar, while other characters all argued against such relationships. In particular, these are the structure of the third premolars, the nature of replacement of the milk premolar (the peculiar "double" replacement of Macropodidae is absent and specialization of $P_3$ has proceeded in the opposite direction) and the structure of the masseteric fossa together with the absence of a masseteric canal. The case for special thylacoleonine affinities is equally slender and rests upon no more than the enlarged sectorial, a character which is likely to be convergent since the teeth of the "plagiaulacoid" type have been developed independently by at least phalangers, macropods, caenolestoids, multituberculates, and tarsioids (Simpson 1933).

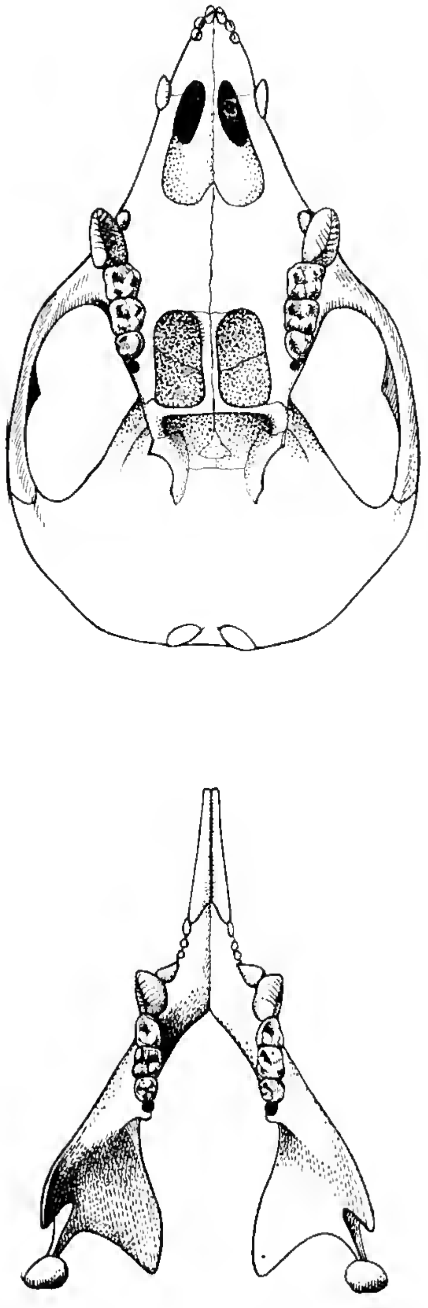


Fig. 11.—*Burramys parvus*. Occlusal views of restored cranium and mandible (from Ride 1956). x 2.5.

It is very probable that *Burramys* is a member of an aberrant line of Phalangerinae possessing some relatively unspecialized characters, e.g., a *Distoechurus*-like palate and quadricuspid bunodont molars, but also some very specialized ones such as large grooved sectorials, reduced fourth molars, and elongate incisors, characters which probably point to some peculiar insectivorous (or microcarnivorous) adaptation.

### Macropodidae Gray, 1821

As many fossil species of the family of kangaroos and wallabies have been described as all other Australian fossil marsupials put together. To anyone who knows our present marsupial fauna this is scarcely surprising because, quite apart from their commonness, macropods are generally fairly large animals, are often gregarious and are the dominant herbivores (as they probably were during the Pleistocene as well); it is thus likely that they provided the main source of prey for marsupial lions, thylacines, and other large carnivores (or scavengers) of their time—all are features which are likely to lead to good representation in the fossil record.

In spite of their commonness, or perhaps partly because of it, our knowledge of their taxonomy is more confused than that of other groups and it is clear that Simpson's (1930, p. 69) hope that this state of affairs would soon be corrected has not yet been fulfilled. The confusion is the result of factors, usual in palaeontology, which are

(a) the uncertainty of generic limits
(b) poorly studied subjective synonymy between named species and poorly stated species limits, and
(c) generally unknown temporal relations between the named species.

### Generic classification

Since almost all fossil Macropodidae are Pleistocene, it is not unreasonable to suppose that the generic limits of the modern Macropodidae will be applicable except in a few cases where whole genera have become extinct as has happened in the Sthenurinae where both *Sthenurus* and *Procoptodon* are no longer extant. However, not only has the generic classification of fossil kangaroos always lagged behind that of modern kangaroos and wallabies, but generic limits among modern Macropididae are still undecided (*see* Ride 1962a for a statement of the positions taken by various authorities in modern times). Fortunately, taxonomic activity is such that investigations which are currently in progress of behaviour, chromosomes, blood sera, soft part anatomy, bone, and dentition, will greatly advance our interpretation during the next decade, and then the taxonomist of fossil kangaroos will be in a much better position to produce a comparable arrangement. At present the taxonomist of fossil kangaroos can only place his generic limits by interpreting a limited and imperfect number of characters and without much help from neontological studies which can often lead to much more meaningful interpretation.

Today, the area of most confusion among modern animals is that surrounding the limits of *Macropus*, *Megaleia*, *Osphranter*, *Wallabia* and the other middle-sized wallabies. This confusion is made worse for the taxonomist of modern Macropodidae by the uncertain relationship between the type species of *Wallabia* (*W. bicolor*) and the group of large fossil wallabies called *Protemnodon*; Stirton (1963) has shown that these large fossil wallabies are distinctive, but it is still not clear whether the characters in which they differ from some of the modern wallabies are merely expressions of size increase which alone is scarcely a character upon which to separate genera. The position is made even more unstable by the knowledge that *Wallabia bicolor* differs very greatly in chromosome morphology from other modern middle-sized wallabies and is scarcely likely to be congeneric with them; these may require yet another generic name. At present we can only await the result of further studies to clarify the position; in the meantime it would seem very reasonable for the neontologist to do as most authors do and deliberately ignore the fossils, and also the differences between *Wallabia bicolor* and other wallabies, and use the name *Wallabia* for this group.

It is probable that this deliberate cleavage between neontological classification and palaeontology is desirable for stability in the names of fossils as well. At present the incomplete nature of most material of fossil species precludes its identification with genera which are established by the neontologist upon the characters provided by more complete material. Thus, while taxonomists of modern animals find little difficulty in deciding whether or not a species, or population, belongs with one or other of the hypsodont kangaroos *Macropus* or *Megaleia*, some fossil species can scarcely be so assigned; therefore the taxonomist of fossil kangaroos is forced to adopt wider limits and include both genera together. Since these limits imply equivalence with modern genera to zoogeographers and others, much might be said for the abandonment by palaeontologists of generic names of Macropodidae which possess living animals for type species and fall back on the use of purely fossil species concepts which will be dictated by the nature of the material. Thus, kangaroos with high crowned molars with rapid dental progression and premolars which are early shed (see below), would be distinguished from forms with relatively low crowned molars and with tenacious premolars; these latter forms could be further subdivided into those very large forms with very great premolars which are never shed, and those smaller forms which shed even their premolars in extreme old age.

The most recent classification of the species of fossil kangaroos (Simpson 1930) was regarded by its author as unsatisfactory. In it some species are obviously greatly lumped while others are in monotypic genera which are clearly not comparable. This is a legacy which is the result of the alternating actions of describers (who split) and synthesizers (who lumped). We are now in a describing phase with descriptions being added to a lumped classification, a classification which is due in greatest part to Owen, De Vis, and Lydekker.

The history of this sequence commenced in 1838. Prior to 1863, the date of completion of Gould's Mammals of Australia, the taxonomy of modern Macropodidae as generally accepted in Britain (*see* Owen 1840, and Waterhouse 1846) was uncomplicated containing only three genera *Macropus*, *Hypsiprymnus* (= *Potorous*) and *Dendrolagus*. The five species described by Owen prior to 1873 (*i.e.* 1838-1859) were all included in the first two of these. Of the remaining sixteen species which he described (*i.e.* 1873-1877), one was a potoroine which he included in *Bettongia* Gray 1837, two were placed in *Osphranter* which had been introduced by Gould, one (*M. ferragus*) was placed in *Macropus*, and the remainder were all placed in six new genera (as well as these, Owen even placed in these new genera two of the five species of his early period and the solitary *Macropus*, i.e. *M. ferragus*, of his later period). Owen thus left twenty-one species distributed between ten genera.

Owen was followed by Lydekker who, in his standard work, the Catalogue of the Fossil Mammalia in the British Museum (Natural History) (1887), placed all of these in the four genera *Macropus*, *Sthenurus*, *Procoptodon*, and *Aepyprymnus* (ignoring the status of *Hypsiprymnus* = *Potoreus*). Since we would remove *Aepyprymnus* today to the Potoroinae and *Sthenurus* and *Procoptodon* to the Sthenurinae, Lydekker actually placed all Macropodinae in the single genus *Macropus*.

De Vis followed him, describing fifteen species of Macropodidae and three new genera between 1883 and 1895. These three new genera had one species each and of them one, *Triclis* (= *Propleopus*), is a potoroine while the other two are fragments generically not determinable. The remainder of his species were described as belonging to *Sthenurus* (in which he included *Procoptodon*), *Macropus* which he confined to the hypsodont kangaroos, and *Halmaturus* a name which he applied (actually, misapplied, following others) to all the remainder.

The most recent complete revision is Simpson's (1930) Post-Mesozoic Marsupialia, and again the synthesis produced a lumped taxonomy. In effect Simpson returned to the concepts of Lydekker, except that he recognized *Protemnodon* Owen, and placed all the *Halmaturus* fossils of De Vis into *Macropus*.

Today we have thus a classification of fossil kangaroos which is excessively lumped when compared with the generic classification of Recent forms. The only Macropodinae outside *Macropus* are *Brachalletes* De Vis and *Synaptodon* De Vis which are probably not determinable, and *Protemnodon* which is confined to an uncertain number of very large, large-premolared fossil wallabies; and the newly described *Prionotemnus* Stirton (1955) which has not yet been satisfactorily compared with any other genera.

### Structure and Terminology in Macropodidae

Descriptions of fossil macropod species are particularly difficult to evaluate and this leads to uncertainty in subjective synonymy. In the main these descriptive complications are due to nature of the macropod skull and dentition and in particular to its ontogenetic processes, but they are also unduly confused at present by the existence of more than one set of dental terminology.

Like the Phalangeridae from which they were clearly derived, the Macropodidae possess quadricuspid molars but, unlike most of them, these are often further complicated by the development of lophs, links, and folds of enamel which increase their efficiency as grinders. Canines are generally absent and, as in Phalangeridae, incisors are reduced to three above and a single pair below. However, the acquisition of a grazing habit and the development of elongate sectorials has resulted in the elaboration of the masseteric musculature and in particular a masseteric foramen is developed in the mandible (*see* Ride 1959). Premolars have been reduced to two only in the permanent series and with this has come a unique sequence of replacement in which the most posterior permanent premolar supplants not only its milk predecessor but also the preceding permanent tooth. Since both permanent teeth are elaborate sectorials (or are derived from them) while the milk tooth is a molariform tooth, the macropod toothrow always comprises a sectorial followed by a row of molariform teeth. In *Hypsiprymnodon* alone of the Macropodidae both permanent premolars have a brief coexistence in fully erupted state (Woods 1960, Ride 1961). Complexity does not end here, however, because in many Macropodidae the molar tooth-row moves bodily forward during the life of the animal (fig. 12) with the result that the position of various teeth in relation to various cranial features are progressively altered, and even the angles of the various teeth and their longitudinal dimensions change. Further, the permanent premolar (and even succeeding molars) may be shed from the front of the jaws as in the great kangaroos, or molars may be impacted and shed laterally from behind the permanent premolar as in some wallabies. Since characters such as the relative positions of teeth to bony processes, and even the degrees of development of these in Macropodidae, are so very dependent upon ontogenetic stages, they are very difficult to interpret when they are used in descriptions which involve insufficient material to establish the various developmental sequences.

Differences in the terminology of premolars applied by two schools of dental nomenclature are nowhere more obvious than in the taxonomy of Macropodidae since the characters of the two permanent premolars are often diagnostic. One school holds that since more than three permanent premolars have not been discovered in known Marsupialia these should be numbered 1, 2, 3. The other school (of which I am one, and I have consistently applied the 1, 3, 4 nomenclature in this review) notes that since Marsupialia and Eutheria are probably monophyletic and that Eutheria possess up to four premolars, known Marsupialia have probably lost one. The last tooth with a predecessor (i.e., the most posterior premolar) is always in contact with the first molar (unless, as in some Dasyuridae, it is absent), accordingly this is called 4 and is regarded as homologous with the fourth premolar of Eutheria and Triconodonta. This conclusion was adopted by Thomas whose 1888 Catalogue forms the foundation of all modern taxonomic work on marsupials; by Lydekker whose Catalogue (1887) summarizes and synthesizes Richard Owen's work; by H. H. Finlayson, E. Le G. Troughton and G. H. H. Tate whose monographs on Australian Marsupialia together make up the greater part of all modern taxonomic work on this group; and by C. W. De Vis who, second only to Richard Owen, was responsible for the greater part of the descriptive literature on fossil Macropodidae. The other two premolars are called by this school P3 and P1 in accordance with the observation that there is most usually a gap between the most anterior and the intermediate premolars.

While two schools of premolar terminology have been in existence for some time (the literature of American marsupials generally applies the P1, 2, 3 terminology) a second school of incisor terminology has only lately arisen. It was introduced by Stirton (1955) who used

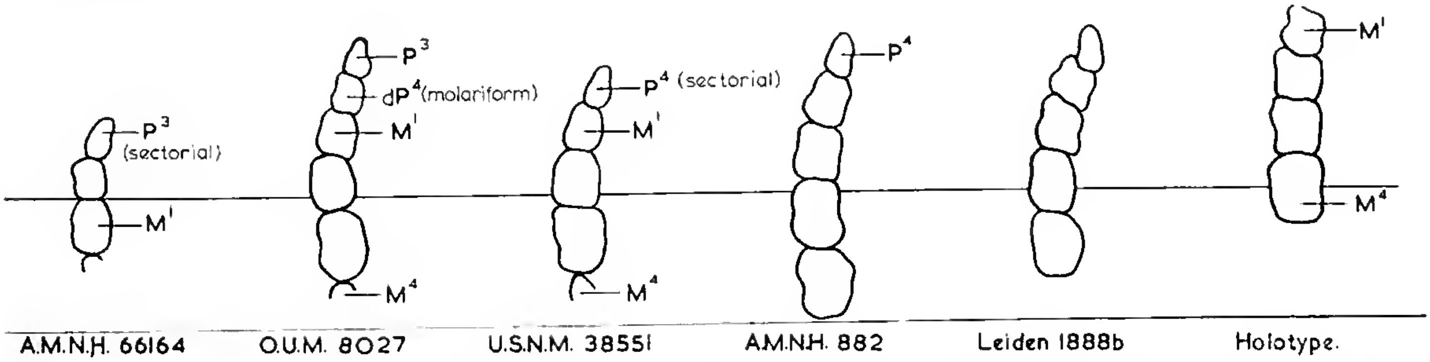


Fig. 12.—The succession and forward movement of cheek-teeth of Macropodidae illustrated by the modern wallaby *Protemnodon parma*. The transverse line indicates the position of the tips of the descending zygomatic processes of the maxillae. The youngest individual is on the left, and the oldest is on the right (after Ride 1957).

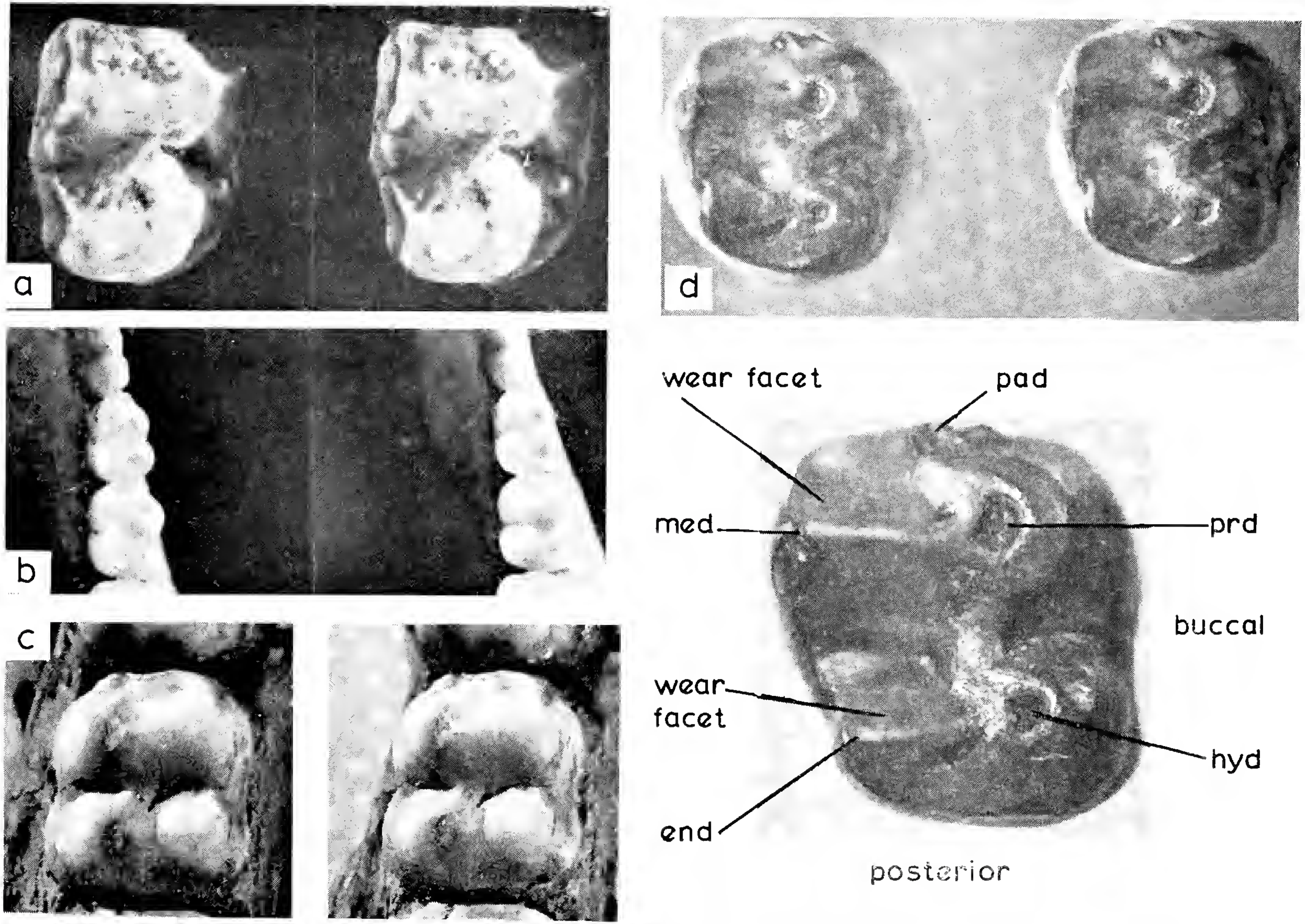


Fig 13.—The Grange Burn molar, and stereo-pairs of other molar teeth for comparison. (a) *Phalanger nudicaudatus* rt. $M^2$. (b) *Potorous gilberti* rt. $M_1$, $M_2$. (c) *Propleopus oscillans* left $M_2$ of holotype (photograph by courtesy of Qd Mus.). (d) Grange Burn tooth. Stereorelief and scale not uniform

the names $I^{2\ 3\ 4}$ for the upper incisors and $I_2$ for the lower, in place of the usual $I^{1\ 2\ 3}$ and $I_1$, stating at the time that this was based upon the assumption that the primitive incisor formula in marsupials is $\frac{1 \cdot 2 \cdot 3 \cdot 4 \cdot 5}{1 \cdot 2 \cdot 3 \cdot 4 \cdot 5}$ and that the remaining incisors of the Macropodidae are $\frac{0 \cdot 2 \cdot 3 \cdot 4 \cdot 0}{0 \cdot 2 \cdot 0 \cdot 0 \cdot 0}$. Stirton has since (1963) abandoned this terminology, but Marcus (1962) has adopted it. I have reviewed (1962, pp. 297, 8) the embryological evidence for the primitive incisor formula in marsupials and there is little doubt that evidence exists which suggests that the formula is at least six in the upper jaw. It is also likely that the diprotodont lower incisors are the third or fourth teeth of the series. In spite of this, I would not at present advocate the introduction of a further incisor terminology to upset that which is in almost universal use until the fossils are found which demand it.

Phyletic lines in Macropodidae

Today, there appear to be three phyletic lines of Macropodidae. One of these, the Potoroinae (Hypsiprymnodontinae and Potoroinae of earlier authors—*see* Woods 1960) appears to be an early offshoot combining a number of primitive characters (such as a hallux and simple alimentary canal in *Hyprispymnodon*, and relatively simple molars in most of the group), with a number of extreme specializations (like anterior vaginal expansions, plagiaulacoid premolars, and enormous masseteric canals. See Pearson 1949, Woods 1960, Ride 1961).

The most modern of the offshoots from the main stem is the Sthenurinae. These are secondarily adapted for browsing from the main grazing line (*see* Ride 1959) and culminate in *Procoptodon* with deep, heavy mandibular rami, broad crushing premolars, wide highly "ornamented" molars, erect lower incisors, reduced upper incisors, elongate descending zygomatic processes of the premaxillae, and a coossified mandibular symphysis.

The Macropodinae are the stem forms of the radiation. At their most highly evolved they are supremely modified for grazing and swift cursorial (saltatory) existence. However, within the Macropodinae numbers of different kinds of modification are visible; some of them are small animals with scarcely any of the grazing modifications we associate with the group (e.g., *Lagostrophus*, see Thomas 1887) while others are large grazers which place almost no dependence upon their sectorial premolars and shed them early, meeting all their masticatory requirements with a rapidly progressing molar row. In these "end forms" molars are hypsodont to meet the abrasive effects of silica-containing grasses and, like those of their eutherian counterparts, lophodont molars have links which increase the efficiency of their grinding surfaces. Some Macropodinae have enlarged sectorials almost to the extent of the Potoroinae. In the past some of these forms with large sectorials were very large (e.g., *Protemnodon*) but today they are generally of moderate size and include the forest and thicket dwelling wallabies and tree-kangaroos (*Wallabia bicolor*, *Dorcopsis*, *Dorcopsulus* and *Dendrolagus*); these Macropodinae possess simpler molars than their grazing adapted relatives.

Until recently, *Palorchestes* was believed to be a giant kangaroo, however revision by Woods (1958) has shown unequivocally that this genus represents a slenderly built line of Diprotodontidae which possibly bears to the heavily built Diprotodontinae the same relationship as the eutherian tapirs do to the rhinoceroses.

At present it is not possible to provide a detailed arrangement of fossil kangaroos because proper comparison has yet to be made between the confused samples described from the various strata of the Darling Downs and the various species described by Owen. Revisions of fossil taxa of Macropodidae, or parts of them which have been completed in recent years are of *Sthenurus* (Bartholomai 1963, Marcus 1962), *Protemnodon* (Stirton 1963), *Propleopus* (Woods 1960). However, one form does require special comment because it has to date been referred to the Phalangeridae and (as a cuscus) has even taken its place in palaeoclimatic speculation (Gill 1957, p. 159; 1961, p. 336). This is the fossil tooth from Grange Burn.

## The Grange Burn Potoroo

The Grange Burn Potoroo is one of the most tantalizing of fossils. It is possibly Pliocene and comprises a solitary enamel cap of a macropod second or third right lower molar (Nat. Mus. Vict. No. P 15777). It was collected by Edmund D. Gill, of the National Museum, in the bank of Grange Burn, one mile upstream from Forsyth's Bank, near Hamilton, Victoria. It came from a fossil podsol 6 ins. below basalt, where the Burn flows off the basalt on to Tertiary rocks. Gill (1953a, 1957) regarded the tooth as being cuscus-like and Stirton (1957) agreed, comparing it with the second and third right upper molars of *Phalanger maculatus* and *Ph. orientalis*. He noted that the main difference between the fossil and the cuscuses was that the fossil was larger, more elongate, and possessed a "prominent median lingual inflection"; he regarded the tooth as being much too worn to show any indication of the crenulated surface typical of the *Phalanger* tooth.

Comparison with a wider range of diprotodonts reveals that the tooth is undoubtedly that of a potoroine. It is inseparable in general morphology, positions of wear facets, and patterns of exposed dentine from modern *Potorous* but it is very much larger having about twice the linear dimensions of equivalent teeth of *P. gilberti*. It is as distinct from the other potoroines *Bettongia*, *Caloprymnus*, and *Aepyprymnus* in size as it is from *Potorous*, but detailed comparison of cusp patterns with these has not been made. It is distinguishable from *Propleopus* in its smaller size, more acute lingual cusps, complete absence of a median longitudinal valley, and in its inequality between anterior and posterior transverse dimensions.

The fossil tooth (fig. 13) has four cusps: two of these, the protoconid and hypoconid, are low in relief and rounded (protocone and hypocone of Stirton 1957, p. 122) while the other two, the metaconid and entoconid, are high and angular (paracone and metacone of Stirton). As measured from the base of the enamel to the tip of the cusp, only the protoconid is really lower than the others (prd 3.3 mm, med 3.9 mm, hyd 3.8 mm, end 3.9 mm), but the relief of the occlusal surface is such that the two sharply angled lingual cusps appear to stand above their rounded buccal counterparts. There are two clearly-defined flat areas at opposite ends of the periphery of the tooth which are, without doubt, areas of contact with adjacent teeth in the tooth-row. Of these, the anterior is broadest and from its buccal edge a broad, shallow channel rises onto the occlusal surface of the tooth to separate off a small "antero basal cingulum" (more properly this channel is the remnant of the entrance to the trigonid basin between protoconid and the almost completely reduced paraconid, see Ride 1961). Dentine is exposed in small sub-circular areas at the tips of the buccal cusps and there are also three smaller dark patches in other places on the occlusal surface which almost certainly mark the presence of fissures or pits in the enamel; the most prominent of these lies postero-buccal to the entoconid and represents the posterior part of the talonid basin (*see* Ride 1961, pp. 56, 7).

The occlusal surface of the tooth shows only moderate wear; the posterior surfaces of the semi-lophids (*i.e.* the areas which lie posterior to the transverse ridges which run from the acute metaconid to the rounded protoconid, and from the acute entoconid to the hypoconid) are covered with enamel which has a faintly pitted surface which is obviously quite unworn since it lacks facets, or the microscopic scratches which are typical of dentally abraded surfaces. However, in contrast, the anterobuccal faces of the metaconid and entoconid have well marked wear facets with pronounced microgrooves; these wear facets have not passed through the enamel into the dentine beneath. Wear through to the dentine is only present on the tips of the two buccal cusps; here, more or less circular areas of dentine are exposed. The rounded buccal shoulders of these cusps are also well-marked with microgrooves and in particular, these are concentrated in slight facets anterobuccal and posterobuccal to each cusp.

The length of the tooth from anterior to posterior contact areas is 8.3 mm, breadth at level of anterior cusps 7.8 mm, and breadth at level of posterior cusps 6.4 mm.

Since other authors have regarded this tooth as being most like a right upper molar of *Phalanger* while I regard it as being a right lower molar of *Potorous*, differences between these teeth are rather important (fig. 13a, b) and are tabulated here.

Rt $M^2$ *Phalanger (nudicaudatus* and *maculatus)*

1. All cusps sharply angular.
2. Wear facets on posterior faces of semi-lophids.
3. When wear is at the stage where dentine shows through the tips of lingual cusps only and not through the buccal cusps, the anterior faces of the semi-lophids are deeply ridged with crenulated enamel.
4. As the tooth wears, the area of exposed dentine spreads anteriorly and posteriorly from the tips of the lingual cusps to form two Vs along the antero-postero ridges. After this stage it begins to spread buccalwards along the transverse ridges of the semi-lophids.
5. The antero lingual face of the protocone is flattened and facet-like. There is no antero basal cingulum.
6. There is no fissure posterior to the transverse ridge between hypocone and metacone.

Rt. $M_2$ *Potorous (gilberti)*

1. Lingual cusps angular, buccal cusps rounded.
2. Wear facets on anterior faces of semi-lophids.
3. When only two of the cusps (i.e. the low rounded buccal cusps) show exposed dentine there is no crenulated enamel on any faces of the tooth.
4. As the tooth wears the area of exposed dentine at the tips of the two rounded buccal cusps spreads transversely across the tooth, not anteroposteriorly until after the pairs of transversely placed cusps become joined.
5. The antero buccal face of the protoconid carries a broad shallow channel which opens out onto the occlusal face of the tooth, separating a small "antero basal cingulum".
6. The posterior part of the basin of the talonid is represented by a fissure in the enamel, posterior to the transverse ridge between the posterior cusps (end & hyd).

The Grange Burn fossil possesses all the characters of the *Potorous* molar and none of those of *Phalanger*.

The only fossil potoroine which approaches the Grange Burn fossil in size is *Propleopus oscillans*. Woods (1960, p. 201) gives dimensions of the lower molars of two specimens of *P. oscillans* as being $M_1$ 9.5 x 8.7 and 9.3 x 9.2, $M_2$ 10.8 x 9.8 and 10.1 x 10.0, $M_3$ 11.2 x 10.3 and 10.7 x 10.2 mm; the Grange Burn fossil measures 8.3 x 7.8 mm. There are also considerable resemblances in general morphology. Comparison with stereoscopic pairs provided through the kindness of Mr. J. T. Woods (fig. 13c) reveals that the *Propleopus* lower molar differs in having more rounded lingual cusps, a more pronounced median longitudinal valley (defined Ride 1961, p. 56, under $M_2$) which is completely lacking in the Grange Burn fossil but visible in all molars of the holotype of *P. oscillans*. The molars of *P. oscillans* also seem much more square (except $M_1$ and $M_4$ which the Grange Burn fossil cannot be: it is not $M_1$ because the anterior moiety is broader than the posterior moiety and is not $M_4$ because there are contact surfaces at both ends of the tooth).

Since the differences between the Grange Burn fossil and *P. oscillans* are slight and are certainly no greater than those between related species in other genera of Macropodidae it is not possible to decide with any degree of certainty whether this single tooth should be placed in *Propleopus* on grounds of size, or whether it should be regarded as a gigantic *Potorous* on grounds of morphological similarity. It seems safest to conclude, for the present, that it is a potoroine and leave naming it until further material is discovered. The present tooth contains sufficient features to be certain that the species is new, but it will require the discovery of a fourth molar or a premolar to provide sufficient diagnostic characters to name the genus.

### Diprotodontidae Gill, 1872

The Diprotodontidae are the giants of the Australian fossil record. These great quadrupedal herbivores are well represented in the fossil record as far back as the Miocene. Unfortunately, there has been no modern synthesis of the group (which is now known to contain two divergent phyla, the lightly built *Palorchestes*-like forms and the more typical diprotodontids) and the status of a number of the species, e.g. *D. minor*, *D. bennetti*, *D. longiceps*, is not clear from the literature. De Vis (1891b) provides a key to the genera; he also considers that *Sceparnodon* probably belongs here (see under Vombatidae).*

The most valuable statements of the temporal distribution of diprotodontids are in surveys by Woods (1960a, 1962) and data selected from these are tabulated below. In this table many formations and localities are omitted to avoid duplication but sufficient are given to indicate the diprotodontid faunal associations, and the distributions of various species. As Woods suggests, it seems likely that Diprotodontidae will prove to be stratigraphically important.

| Age | Formation, etc. | Species |
|---|---|---|
| Recent .... | Tartangan culture BP 6,570 | *Diprotodon optatum* |
| Pleistocene | Mowbray Swamp, Tas. | *Nototherium tasmanicum*<br>*N. mitchelli* |
|  | *Diprotodon* Beds, Darling Downs, Qd. | *Diprotodon optatum*<br>*Nototherium mitchelli*<br>*Palorchestes azael*<br>*Euowenia robusta.* |
| Pliocene | Otibanda Lake Beds, N.G. | *Nototherium watutense* (? *Meniscolophus*) |
|  | Chinchilla Sand, Darling Downs, Qd. | *Euowenia grata*<br>*Euryzygoma dunense*<br>*Palorchestes parvus*<br>*Diprotodon* sp. (Woods 1962, p. 46) |
|  | Mampuwordu Sands, S.A. | *Meniscolophus mawsoni*<br>*Euowenia*-like form |
| Miocene | Cheltenhamian Stage, Vic. | *Nototherium* (premolar figd Stirton 1957 see Woods 1962, p. 45)<br>Diprotodontidae. Maxillary and mandibular fragments |
|  | Etadunna Fm., S.A. | Small diprotodontid with ?Palorchestine affinities (Stirton *et al* 1961, pp. 36, 7) |

*Note:* The sequence of the formations within each age does not necessarily indicate temporal succession.

The Otibanda Lake Beds were formerly thought to be Pleistocene but parts of them are probably Upper Pliocene. Stirton (1963, footnote to p. 144) gives a K. A. date of 4·5 million years for pyroclastics associated with them.

### Vombatidae Iredale & Troughton, 1934.

The origin of wombats is unknown although their diprotodonty and syndactyly clearly indicate that they are Diprotodonta. Dental characters are aberrant in them and give little real clue to their relationships with other families in the order. Various attempts have been made to elicit affinities from these and other anatomical features, and Tate (1951, p. 3) has reviewed this work.

No Tertiary wombats have yet been described and no fossils are reported as having been collected in the various deposits of this age investigated by Stirton in Central Australia or Victoria. Woods lists none from the Chinchilla Sand (Woods 1960a, 1962) nor does De Vis (1891) although the general term "Darling Downs" which he uses for Queensland wombats may include this Pliocene formation.

The most recent revision of the wombats is by Tate (1951) who dealt with both fossil and recent forms. This work, when taken together with Lydekker's (1887) catalogue (to which Tate does not refer), provides a very adequate summary of present knowledge of the fossils. However these two works differ slightly in arrangement. Lydekker's list is most useful in providing concise descriptions and a synoptic view of Owen's fossil species, but it should be read in the light of De Vis' further revision of the status of the species *P. mitchelli* and *P. thomsoni* (De Vis 1891). In his arrangement, Lydekker adopts a classification which is that used for modern wombats today, i.e. he recognizes two main kinds of normal-sized wombat (the plains-dwelling *Lasiorhinus* wombats and the *Vombatus* species of the more densely timbered country) although of course he uses only the name *Phascolomys* which was then in general use for them all. He employs *Phascolonus* for the Pleistocene Giant Wombat.

Of the fossil wombats known today, Lydekker's revision omits only *P. hacketti* Glauert, 1910, *P. angustidens* De Vis, 1891 (which were described since) and *P. pliocenus* McCoy, 1874 (which was not noticed by him). Tate places *P. hacketti* and *P. pliocenus* with *Vombatus*, and *P. angustidens* with *Lasiorhinus*. Both Tate and Lydekker exclude *P. curvirostris* from these two groups; Lydekker regarding it as *incertae sedis*, while Tate creates a new genus, *Ramsayia*, for it. Tate regards the position of *P. medius* Owen and *P. magnus* Owen as uncertain, Lydekker includes them in the *Vombatus* group.

*Phascolonus*, the genus of Giant Wombats, is universally accepted and is now known from very much better material than Lydekker or Owen possessed; this is from Lake Calabonna (Stirling 1913). The genus *Sceparnodon* is conventionally placed in synonymy with *Phascolonus*, but with some reserve (Tate 1951, p. 12) because of De Vis' (1891a) strong arguments that these were not synonymous and moreover were not even closely related. He regarded *Sceparnodon* as being diprotodontid (*see* above above under Diprotodontidae).

### MARSUPIALIA *incertae sedis*

### Notoryctidae Ogilby, 1892.

*Notoryctes*, the marsupial mole, is unknown as a fossil and it is so highly specialized in dentition, skull structure, and limb structure that arguments as to its affinities which are based upon these features can only produce tentative results. It is usual to follow Stirling's (1891) original conclusions and relate it to the

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* Since this address was given Stephenson (1963) has endorsed this conclusion and has, in addition, described a new species and genus of diprotodontid, *Diarcodon parvus*.

Dasyuridae (*see* Wood Jones 1923, and Simpson 1945). However, Bensley (1903, p. 173) regarded the foot structure of *Notoryctes* as being derived from "one of ordinary phalangerine type" and its dentition as having been "so modified away from the usual dasyurid and peramelid type that it does not present any of the special characters which distinguish the dentition of these two families" (Bensley 1903, p. 117). Accordingly he placed *Notoryctes* (p. 210) in the "polyprotodont syndactyla" with the Peramelidae. Cabrera (1919, p. 90) followed Bensley. Van der Klaauw (1931, p. 254) has pointed out that the structure of the tympanic in *Notoryctes* agrees more with Diprotodonta than with other marsupials. Some authors (e.g. Troughton 1959, p. 75) have preferred to remain uncommitted and, in view of the introduction of ordinal classification here, it seems wisest to follow them.

### The Australian Radiation—Origin, Isolation and Drift.

The Australian radiation, by comparison with mammal radiations of other inhabitable land masses, is unbalanced in the degree in which various major taxa of terrestrial mammals (and in particular Cohorts) are represented in it. Thus, with the exception of the dingo (an obviously Pleistocene, or Recent, introduction), Ferungulata are absent but represented in all others; Unguiculata (except for flying forms such as bats) are absent but present in all others; and Glires, while present, are confined to representation from a single suborder of Rodentia (and a single family of these) when other continents have representatives of both orders and all suborders.

The explanation of this can only be that the Australian Continent has been through a very long period of isolation which has lasted through much of the Age of Mammals. However, in this isolation, Australia has developed a wide and comprehensively diversified mammalian fauna, almost entirely marsupial, which has paralleled the mixed marsupial and eutherian radiation of South America, and pure eutherian radiations of other continents, in almost all of the kinds of niche available to mammals. Thus, while in South America the marsupials provided the carnivorous predators and smaller insectivores and carnivores, the archaic ungulates of that continent provided the herbivores (*see* Simpson 1950), in Australia all three main adaptive avenues were filled with marsupials. Moreover, they were not interrupted by invasions of similarly adapted mammals from outside during this period (or if they were the invaders were repelled leaving no trace).

During the early part of this century many responsible zoologists believed that the long isolation of Australia, taken together with the fact that the greater component of the Australian fauna was marsupial and similar to that of South America, could best be explained by the theory of Continental Drift. Further, palaeontologists working on South American marsupials argued for the existence of special relationships between separate parts of the South American Marsupial fauna and parts of the Australian fauna; in particular between *Thylacinus* and Borhyaenidae, and between Diprotodonta and Paucituberculata. I have reviewed this work, and that of others, and conclude that these relationships cannot be supported (Ride 1962).

Most zoologists today believe that an alternative explanation, due principally to W. D. Matthew and G. G. Simpson, is more reasonable; this states that Australia has been no more isolated during the whole of the Age of Mammals than it is today and during this period entry to it has been by a combination of chance and rafting ability across the water gaps of the Malaysian archipelago. Thus, it is the effect of chance which has led to the imbalance of the Australian fauna. In contrast, many botanists (*see* Good 1963, but also see Burbidge 1960 p. 156 for expressions of reserve) would not agree with this conclusion and still hold to the theory of Continental Drift, observing that the short distance across Torres Straits marks a greater floral discontinuity than any similar distance on the earth's surface and moreover floral continuity with the archipelago occurs through New Britain, the New Hebrides and New Caledonia and, allowing for differences of latitude, even to New Zealand; they conclude therefore that the floral discontinuity can best be explained by the hypothesis that the gap between Australia and New Guinea has only become narrowed by the northward drift of the Australian continent.

In recent years geophysical work on palaeomagnetism supported by data of palaeoclimatology (*see* Runcorn 1962, Nairn 1961) have made it reasonably certain that Continental Drift has occurred. The direction of the magnetic field of rocks of known age on a single continent can be plotted to give a polar wandering curve for that continent which probably indicates the positions of the magnetic poles at various ages relative to it. It is now known that polar wandering curves of the various continents do not agree and that the pole positions given by various continents for any particular age can only be made to agree by displacing the continents relative to each other, i.e., by "drifting" them. Until very recently, it was not known whether Continental Drift as postulated from these data occurred late enough in time for it to effect the composition of the Australian Mammal fauna. However, the work of Irving *et al* (1963) have made it abundantly clear that Australia only achieved its present latitude during the late Tertiary and that since the Mesozoic it has been moving slowly northwards across what is now the Southern Ocean.

It seems that as biologists we are now in the fortunate position of having a very reasonable working hypothesis which has been erected solely on non-biological data and which we can now test by biological observation. Fossil marsupials do not yet help us; such marsupials as have yet been found in New Guinea are Pleistocene and upper Pliocene (Stirton 1963, Woods 1962) while the distribution of modern marsupials in New Guinea and the adjacent islands is entirely consistent with its being the product of alterations in Pleistocene sea level, and even through chance distribution across very short water barriers over a very short space of time.

On the other hand a very wide water gap between Australia and Asia during much of the Tertiary is supported by the apparent lack of success enjoyed by non-marsupial invaders before at least the Miocene (the Muridae first appear in the fossil record in the Pliocene of Europe and Asia). During the early Tertiary, Asia certainly possessed such highly efficient short water-barrier crossers as Primates, Insectivora, Sciuromorpha, Hystricomorpha, etc. After all, even elephants succeeded in crossing into Celebes and across Wallace's Line into Flores during the Pleistocene (Hooijer 1962).

### Added in Proof

Since this address was submitted for publication, a number of articles with important bearing on it have come to my notice. These are by Chow (1963), Hofer (1952), Hooijer (1964), Kean, Marryatt & Carroll (1964), Macintosh & Mahoney (1964), Mahoney (1964), Mills (1964), and Stephenson (1964).

The nature and character of ancestral marsupials (see Fig. 1 and under Phylogeny) are clarified by J. R. E. Mills whose work (1964, *Proc. Linn. Soc. Lond.*, Vol. 175, pp. 117-133) would indicate common ancestry of Eutheria and Marsupialia among the Amphitheriidae of the Upper Jurassic. Formerly, inadequate material of Pantotheria led Simpson (1945, pp. 169, 70) to state that "Despite a general resemblance, the dental differences in detail [between pantotheres, marsupials and eutherians] are great, and various attempts to homologize molar cusps or to specify closer affinities are so contradictory and hypothetical as to provide no worth while data for taxonomy." Now, however, newly prepared specimens of *Peramus* and *Amphitherium* from the Upper Jurassic suggest that the relationship is closer than hitherto suspected and that the molar pattern of Amphitheriidae (in which Mills includes *Peramus*) is well on the way to the tribosphenic condition characteristic of both marsupial and placental lines in the Upper Cretaceous. Mills is of the opinion that, on purely dental evidence, the division between marsupial and placental could date from this stage. In connection with marsupial dental homologies (see under Macropodidae—Structure and Terminology) it is of interest to note that specimens of *Peramus* examined by Mills possess a canine, four premolars, and four molars; specimens of *Amphitherium* also possess four premolars and five molars, although Mills notes that up to seven molars are known in specimens not seen by him.

R. I. Kean, R. G. Marryatt & A. L. K. Carroll (1964, *Aust. J. Zool.*, Vol. 12, pp. 18-41) have also added data relevant to Kean's earlier argument that the marsupial female urinogenital system is derived from the eutherian condition. They report the presence of epithelial cells lining the median "pseudovagina" of a large series of *Trichosurus vulpecula* and conclude that this epithelium acts as a retarding influence in the closure of the canal after parturition; they are of the opinion that this lining is vestigial and not rudimentary, hence marsupials with a permanently lined, and open, median canal are, in their opinion, primitive.

The taxonomic status of *Dasyurus affinis* (see under Dasyuridae) has been settled by J. A. Mahoney (1964, *Proc. Roy. Soc. Vict.* Vol. 77, pp. 525-533). Both syntypes, in mensuration and morphology, fall within the range of variation of *Dasyurus maculatus*, a modern species.

N. W. G. Macintosh and J. A. Mahoney (1964, *Proc. Roy. Soc. Vict.* Vol. 77 pp. 507-514) have also added to the complexity of the *Thylacinus* problem by recording a small Thylacine molar from Fromm's Landing in the Murray Valley, South Australia. This tooth comes from a horizon dated at between 1806 ± 85 B.C. and 1931 ± 85 B.C. It is the first small *Thylacinus* tooth (the measurement of $M^1$ pr.-me. which these authors give is less than any of the south-western cave Thylacines measured by me) to be recorded to the east of the Nullarbor in an area which is otherwise occupied by the larger form. The tooth is also morphologically unusual in that the protocone is divided.

The identity of *Sceparnodon* (see under Vombatidae and Diprotodontidae) has been clarified by N. G. Stephenson (1964, *Proc. zool. Soc. Lond.* Vol. 142, pp. 537-546). He concludes that it is a member of the Diprotodontidae. Stephenson also expresses the opinion (p. 540) that the only specimen known of *Phascolomys curvirostris* (see under Vombatidae) is possibly a badly eroded rostrum of *P. magnus* "or at least of a member of the wombat series of comparable size to this species". Stephenson has also (1963, *Palaeontology* Vol. 6, pp. 615-624) commented on the distinctness of *Sarcophilus laniarius* and *S. harrisi* (see under *S. laniarius*—Dasyuridae); his measurements of two specimens of *laniarius* and of one of *harrisi* (p. 618) do not support differences in size claimed for them by other authors.

Earlier (1962), I had drawn attention to the fact that, in the absence of Asiatic marsupials, the presence of the notoungulate *Palaeostylops* in the Palaeocene of Mongolia was evidence that a migration route between South America and Asia was open in the early Tertiary. Chow Min-Chen (1963, *Scientia Sinica*, Vol. 12, pp. 1889-1893) has now described a possible megalonychoid xenarthran (*Chungchienia sichuanica*) from the Eocene of Honan. Megalonychoids are unknown outside South America until the Pliocene (Simpson 1945, p. 69). D. A. Hooijer (1964, *Zool. Meded.* Vol. 40, pp. 37-44) has published further information on the pygmy stegodont from Flores. He says that it is similar in size to the species known from Celebes but regards it as unlikely that both are conspecific. The material from Flores comprises two milk molars.

Finally, I am indebted to Dr W. D. Turnbull of the Chicago Natural History Museum for bringing to my notice Helmut Hofer's remarkable "Über das gegenwärtige Bild der Evolution der Beuteltiere" (1952, *Zool. Jb. Abt. 2.* Vol. 72, pp. 365-437) and to Mrs. A. Neumann for translating it. While he reviews no original work on Australian fossil marsupials more recent than that of Wood Jones on *Wynyardia*, Hofer gives much interesting speculation on the origin of the various marsupial phyla and, in particular, he summarizes the work of various German anatomists and embryologists which is not generally known to readers of the more usual literature on Australian marsupials.

Hofer bases most of his speculation and review of American marsupials on the work of Simpson, and of Australian marsupials on Bensley and Tate. He concludes that, despite lack of fossils, dasyurids are certainly derived from didelphoids, and that borhyaenoids are distinct from *Thylacinus*. He regards the perameloids as a very early lateral branch of the south-east Asian or Australian dasyuroid- or didelphoid-like marsupials, paralleling the South American *Caroloameghinia* among didelphoids. The origin of diprotodonty receives particular attention because of Hofer's own interest in masticatory musculature. He regards shortening of the mandible by mutation as a necessary step and cites modern experimental work with dogs to show that such a step is not only possible, but can also be functional. He is of the opinion that this mutation could have been of frequent occurrence among didelphoids and that this has led to the parallel development of diprotodonty in Caenolestoidea and Phalangeroidea. He supports this view with the observation that the sectorial tooth in these groups is not homologous, but this has now lost much of its force as the result of de Paula Couto's work of 1952 (discussed in Ride 1962, p. 295) which has shown that this view of the sectorials is no longer tenable.

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## APPENDIX

### Statistical determination of Subspecies

The granting of subspecific status (and hence trinomials) to populations is arbitrary and depends upon the morphological distinctness of populations as a whole; subspecies may not be wholly definable in absolute terms by the characters of each member. Various authors have discussed the statistics of this (*see* Amadon 1949, Simpson 1961, p. 174 and Mayr, Linsley & Usinger 1953, p. 143) giving definitions as lenient as that which requires only 75% of individuals of a subspecies to be determinable from 75% of another, to more rigid requirements such as that of Mayr et al. who require 75% of the individuals of one population to differ from 97% of the other (or 90% from 90%) and Amadon who requires 75% to be separable from 99.9% (or 97% from 97%).

Mayr *et al.* propose the use of the statistic Coefficient of Difference (of samples)

$$(\mathrm{CD}) \quad \frac{\bar{X}_a - \bar{X}_b}{s_a + s_b} \quad \text{where } \bar{X}_a$$

is the higher of the two sample means and $s_a$ its standard deviation.

In this the numerator expresses the distance between the observed means and where this is less than the combined standard deviations the value of CD will be less than 1.0. Using this statistic, Mayr *et al.* require a CD value of 1.28 for separation of subspecies and Amadon would require a CD of 1.9.

As pointed out by Amadon, the use of such a calculation takes no account of the probable discrepancy between observed and actual (*i.e.*, population) means and standard deviations. This matters little where samples are large, but in fossil samples where values are frequently very small, account must be taken of it; or at least it should be made more difficult to achieve significance with small samples than with large ones. Therefore I include confidence intervals in the test which I use here in order to relate these sample values to populations. Since the introduction of confidence intervals imposes upper and lower limits, there are two (population) Coefficients of Difference for each set of observations. These are designated $\mathrm{CD}_1$, and $\mathrm{CD}_2$.

$$\mathrm{CD}_1 = \frac{\left[\bar{X}_a - tn_a\left(\frac{s_a}{\sqrt{N_a}}\right)\right] - \left[\bar{X}_b + tn_b\left(\frac{s_b}{\sqrt{N_b}}\right)\right]}{\left[\sqrt{\frac{(N_a - 1)\, s_a^2}{n_a\, \chi^2_{.025}}}\right] + \left[\sqrt{\frac{(N_b - 1)\, s_b^2}{n_b\, \chi^2_{.025}}}\right]}$$

$$CD_2 = \frac{\left[\bar{X}_a + tn_a\left(\frac{s_a}{\sqrt{N_a}}\right)\right] - \left[\bar{X}_b - tn_b\left(\frac{s_b}{\sqrt{N_b}}\right)\right]}{\left[\sqrt{\frac{(N_a - 1)\, s_a^2}{n_a\, \chi^2_{.975}}}\right] + \left[\sqrt{\frac{(N_b - 1)\, s_b^2}{n_b\, \chi^2_{.975}}}\right]}$$

where: $\bar{X}_a$ is the higher value of the two sample means,

$S_a$ its standard deviation,

$N_a$ the number of observations.

$tn_a\left(\frac{s_a}{\sqrt{N_a}}\right)$ the confidence limit for the population mean with 95% probability ($tn_a$ the value for t with $n_a$ degrees of freedom),

$\frac{(N_a - 1)\, s_a^2}{n_a \chi^2 .975}$ and $\frac{(N_a - 1)\, s_a^2}{n_a \chi^2 .025}$

the lesser and greater values respectively of the 95% confidence limits of the variance ($n_a$ degrees of freedom). See Simpson, Roe and Leewontin 1960, p. 161.

Similarly $\bar{X}_b$ is the lower value of the two sample means, etc.

As mentioned above, taxonomists differ in the value of CD which they would require before recognizing distinct subspecies. In this connection, it would seem to be logical that the area below the curve of a population which the taxonomist should require to be free of overlap from another population should include the whole of the values which occur at greatest frequency, i.e., it should include that part of the curve within the range of 1 standard deviation on both sides of the mean; thus 84% of the population should be quite distinct. Ideally this should be distinct from the whole of any adjacent population but in practice it is probably sufficient that it should be overlap free from 97% of it (i.e., 2 standard deviations from its mean).

Thus, I would regard a population CD value of 1.5 as adequate to establish subspecies.

Procedure.—In order to test two samples for subspecific distinctness:

(a) Compare means of samples (t test) in all variates likely to give significance.

(b) For variates giving significant t values calculate $CD_1$ and $CD_2$.

To interpret Results:

(a) If both $CD_1$ and $CD_2$ are 1.5 or greater the two populations warrant subspecific separation.

(b) If neither reaches 1.5 it is probable that the populations are not subspecifically distinct.

(c) If $CD_1$ is less than 1.5 and $CD_2$ is 1.5 or more then it is not possible with the material at hand to give subspecific recognition although further material might require it.

Comparison of *Thylacinus*.—In comparison between samples of modern *T. cynocephalus* and Western Cave-fossil *Thylacinus*, the observed means of the characters $M^2$, $M^3$, $M^{1-4}$ were significantly different ($P < 0.01$). CD, $CD_1$, and $CD_2$ were calculated for these and are given here.

| | CD | $CD_1$ | $CD_2$ |
|---|---|---|---|
| $M^2$ | 1·21 | 0·48 | 2·23 |
| $M^3$ | 1·04 | 0·32 | 2·10 |
| $M^{1-4}$ | 0·93 | 0·16 | 2·15 |

In the character $M_4$, where the differences between the means approach significance at the 5% level, CD 0.336, $CD_1$ is a negative quantity, and $CD_2$ 1.28.

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# CONTENTS OF VOLUME 47

## Part 1 *(published 24th April, 1964)*

1. The Environment of the Quokka *(Setonix brachyurus)* in the Darling Range, Western Australia. By G. M. Storr. .... .... .... ... .... 1
2. An Ordovician Cystoid (Pelmatozoa, Echinodermata) from Western Australia. By Ida A. Brown. .... .... .... .... .... .... .... .... 3
3. Description of a new Stonefish of the family Synanceidae from Western Australia. By R. J. McKay. .... .... .... .... .... .... .... 8
4. Association of Larger and Planktonic Foraminifera in single samples from Middle Miocene sediments, Guadalcanal, Solomon Islands, south-west Pacific. By P. J. Coleman and R. A. McTavish. .... .... .... .... 13
5. Discontinuous and Presumed Vicarious Plant Species in Southern Australia. By J. W. Green. ... . .... .... .... ... .... 25

## Part 2 *(published 13th July, 1964)*

6. The Woolgorong Stony Meteorite. By G. J. H. McCall and P. M. Jeffery. 33
7. The agamid Lizards of the genus Tympanocryptis in Western Australia. By G. M. Storr. .... .... .... .... .... .... .... .... .... 43
8. On Beryl from Western Australia. By P. L. C. Grubb. .... .... .... 51
9. Contributiones Florae Australiae Occidentalis XIII. By C. A. Gardner. 54

## Part 3 *(published 30th October, 1964)*

10. Notes on the Skulls of Two Western Australian Rodents with a key to the Skulls of the Rodents of Southwestern Australia. By Ernest Lundelius, Jr. 65
11. Effects of Salt, Temperature and Seed Scarification on Germination of Two Varieties of Arthrocnemum halocnemoides. By C. V. Malcolm. 72
12. Ashbed and Nutrients in the Growth of Seedlings of Karri (Eucalyptus diversicolor F. v. M.). By O. W. Loneragan and J. F. Loneragan. .... 75
13. Foraminiferal Evidence for the Paleocene Age of the King's Park Shale (Perth Basin, Western Australia). By Brian McGowran. .... .... .... 81
14. Projasus—a New Generic Name for Parker's Crayfish, Jasus parkeri Stebbing (Palinuridae: "Silentes"). By R. W. George and J. R. Grindley. .... 87
15. Geographical Variation and Distribution of some Birds from Western Australia. By G. F. Mees. .... .... .... .... .... .... .... .... 91

## Part 4 *(published 29th December, 1964)*

16. A Review of Australian Fossil Marsupials. Presidential Address, 1963. By W. D. L. Ride. .... .... .... .... .... .... .... .... .... 97

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